

A STUDY OF THE GENUS *HELICOGLOEA*¹

GLADYS E. BAKER

Henry Shaw School of Botany of Washington University

*Formerly Jessie R. Barr Research Fellow in the Henry Shaw School of Botany
of Washington University*

A paper published by Patouillard in 1892 included amongst the heterobasidiomycetes the new genus *Helicogloea*, represented by a single species—*H. Lagerheimi* Pat. Later Patouillard seemed confused and uncertain as to its true identity and eventually, in a letter to Coker ('20), stated that *Helicogloea* was not distinct from *Platygloea*. In the literature subsequent references are based on Patouillard's work. No one seems to have examined the type. Just as this work was going to press under the name of *Saccoblastia*, Dr. Donald Rogers called attention to the type which is now in the Farlow herbarium. Patouillard's description fails to mention the "sac" or hypobasidium, easily the most conspicuous part of the fructification. From his illustrations one is forced to conclude that although Patouillard was aware of the structure he was unable to interpret it. There can be no doubt as to the real nature of the specimen. Not only is it a good genus but the type of what three years later Möller ('95) called *Saccoblastia*. Since Patouillard's formal description does not include a statement concerning the hypobasidia the genus stands in need of emendation. Accordingly, the recognized species of *Saccoblastia* must be transferred to the older genus, *Helicogloea*.

HELICOGLOEA Pat., emend.

Fructification resupinate, indeterminate, ranging from a very thin film to a layer several mm. thick, mucous-gelatinous or

¹ An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

floccose; hyphae with or without clamp connections, 2–6 μ wide, branched, sometimes anastomosing, attenuated at the septa; basidia heteromorphic, terminal or intercalary in origin; hypobasidia conspicuous, saccate lateral (with one exception) expansions of the basidial primordia sometimes variously constricted, 15–20–58 $\times$ 4.5–8–16 μ ; epibasidia cylindrical outgrowths of the primordia or hypobasidia, expanding apically to the sporogenous portion, articulate-geniculate, 3–4-septate, each segment producing a sterigma and spore, or an accessory appendage eventually tipped by a sterigma and spore, the entire basidium 45–140 $\times$ 4–11 μ ; spores hyaline, ovoid to ellipsoid, often flattened on one side, with a prominent blunt lateral apiculus, 7–19 $\times$ 4–13 μ ; germination by repetition.

Helicogloea is a member of the Auriculariaceae, heterobasidiomycetes which bear basidiospores in linear sequence on transversely septate basidia. The genus, by reason of a curious sac-like appendage produced during basidial ontogeny, has always been noteworthy. Since the first clear morphological account (Möller, '95) several species have been described but little detailed information concerning the developmental cycle has accumulated. Gäumann and Dodge ('28) summarize the situation by saying: "A cytological study of the species is needed for the interpretation of this storage organ which is unknown in other groups of fungi."

In 1895 Möller (*l. c.*) described two species collected during a stay in Brazil. Both possessed the unique saccate hypobasidia. Möller completely delineated the morphology of the genus. Further detailed studies were not made. As apparently Patouillard's material was never questioned, this work of Möller's stood as the standard of the genus *Saccoblastia*, represented by the species *S. ovispora* Möll. and *S. sphaerospora* Möll.

The next record is that of Bresadola ('03), who added a species from Poland, *Helicogloea graminicola*. His description was accompanied by neither detailed studies nor illustrations. Likewise Bourdot and Galzin ('09, '28), who have enlarged the genus by several species and varieties, have contributed only taxonomic observations.

The first collection of the genus in the United States was made by Couch, 1920, in North Carolina. Coker ('20), puzzled by its peculiar characters, which were so suggestive of *Helicogloea Lagerheimi* yet differing in several respects, published a description of the fungus as *Saccoblastia ovispora* Möller var. *caroliniana*. In 1928, in the meantime having consulted Bresadola who supposedly had seen the type of the species in question, he decided to recognize it as an autonomous species, now *Helicogloea caroliniana*. The original description includes a careful morphological account with lucid illustrations.

Linder ('29) announced a new species based on material collected in Cuba, *Helicogloea intermedia*. This remarkable form was found to have two types of basidial development, the so-called "clavate" type in addition to the established saccate one. From his preparations Linder was able to augment considerably the cytological data. But even so they remained far from complete. The condition of his material which had been preserved in 70 per cent alcohol was hardly suitable for critical work.

Helicogloea Lagerheimi Pat. was collected in Iowa during the summer of 1932 by Rogers and later reported by him ('33). He made additional gatherings during the summer of 1934 and at both times killed and fixed samples of a number of collections. It is material from these sources upon which this study is based.

TECHNIQUE

Several collections of fresh material of *Helicogloea Lagerheimi* were available for histological preparations. All of them were killed and fixed in Flemming's weaker fluid. To the fixing fluid for two lots was added 1 per cent maltose. For two others dehydration by a butyl series was employed, whereas the first mentioned were run through Chamberlain's ('32) full alcohol schedule to xylol and paraffin. Those of the maltose-xylol series proved the most valuable for critical stages. However, subsequent examination indicated that variation was due to the particular specimen as much as to fixation. Serial sections were cut at 15, 10, 8, and 5 μ . Various stains were tried but

Haidenhain's iron-alum haematoxylin with a counter stain of phloxine (a 1 per cent solution in 95 per cent alcohol) was used almost exclusively. A few slides were prepared with Fleming's triple stain to serve as a check for the presence of septa at certain points. In addition whole mounts were made of herbarium specimens whenever possible. After these were revived in a moist chamber they were treated with a weak solution of potassium hydroxide and stained with phloxine (1 per cent solution in water).

MORPHOLOGY OF *H. LAGERHEIMI*

The indeterminate fructification of *Helicogloea Lagerheimi* in a living condition, or when it has been revived in a moist-chamber, appears as a thin gelatinous or mucous coat, loosely attached to its substratum of decorticated and well-decayed wood of various sorts. It ranges in thickness from 100 μ to 1 mm. From prepared sections it is evident that the penetration within the substratum is slight. A few scattered hyphal threads are all that appear within the wood cells, and these are never deeper than a few μ .

Morphologically, there is no tissue differentiation into trama and hymenium, but the whole is simply a mass of hyphal and basidial elements loosely interwoven (fig. 19). This composite figure of the fructification as seen in section represents one in which the hyphae are practically parallel, a feature characteristic of lesser developed fructifications. The development of the fruiting body ranges from a thinly spread layer to thicker ones in which the basidial elements are restricted to the upper layer. In moderately developed specimens the fruiting layer may be as much as one-third the total, or in better developed ones as little as one-sixth, as shown by the comparative scales (fig. 20). The fruiting region is the actively growing part, bearing basidia singly at various levels. The individual hyphal cells are typically binucleate. Occasionally some cells are four-nucleate, but this merely indicates a recent nuclear division not yet followed by wall formation (fig. 14a, d). Usually the two processes are concurrent. The nuclei may lie

in close approximation or be widely separated within the same cell. As the cells become more mature the protoplasmic content is reduced, sometimes to only scattered remnants about the nuclei (fig. 14b, c). The mycelium is slightly irregular, characteristically attenuated at the septa, and its individual cells vary considerably in length. Branches arise as lateral outgrowths of a cell and receive daughter nuclei of the parent-cell dikaryon (fig. 15). There are no clamp connections, but the hyphae branch freely. Anastomoses also occur, although there is no evidence to support Linder's contention that such hyphal union carries a sexual stimulus to fructification.

The morphological development of the basidium may be followed in the diagrammatic series, figures 1 to 13 inclusive, and seen in summation in the composite illustration, figure 19. These figures, drawn to a common scale, show the entire cycle. The first indication of basidium production is the cutting off of a terminal hyphal cell, the primordial cell, easily distinguished by its more homogeneous and denser staining protoplasm (figs. 15, 1). It contains two nuclei, descendants of the dikaryon of the subterminal cell. There may be additional basidia produced by proliferation of the subterminal cell (fig. 16), just as shown by Möller in *H. Lagerheimi* and Coker in *H. caroliniana*. After an increase in thickness the primordium pushes out a small lateral protuberance just above the basal septum (fig. 2). This enlarges rapidly to become the "sac," or, as it will be designated henceforth, the hypobasidium, *sensu* Neuhoﬀ ('24) (figs. 3, 4, 5, 6). Into this the two nuclei migrate and subsequently fuse.

Following a rather protracted resting period the fusion nucleus migrates from the hypobasidium, passing back through the primordial cell into the epibasidium, again *sensu* Neuhoﬀ (fig. 7). The latter, an outgrowth of the primordium, may be apparent at an early stage. Furthermore, it may be distinctly elongated at the time the nuclei leave the hypobasidium or it may develop more slowly (figs. 7, 25). Between the primordium and the epibasidium there is commonly a conspicuous crimp or constriction, but never a wall (fig. 17). The epibasid-

ium is usually elongating as the nucleus moves along (fig. 8), and when it has attained its mature length the apical portion thickens and bends over (figs. 9, 10). Accompanying this is a complete evacuation and withering of the hypobasidium. Later the withering includes the primordial part, and eventually it extends to the lower portion of the epibasidium itself (figs. 11, 12). In mounts made with KOH these emptied portions may be quite swollen so that no collapse is apparent, but the regions are entirely drained of protoplasm. The nucleus now divides, the first septum coming in at once. In a short time the two daughter nuclei divide, and the typical segmented basidium is formed with four sterigmata and spores. These are so oriented commonly, through the curvature of the epibasidium, that the sporogenous portion lies procumbent on the surface of the fructification, thereby greatly favoring the chances of spore dispersal (figs. 12, 13). Bends are located below the spore-bearing portion or in it and simply adjust this region for favorable discharge (figs. 23, 63b). Excessively long thickened appendages in place of sterigmata occur frequently, but these eventually give rise to true sterigmata and spores (fig. 67b, c, d). Infrequently the basidia remain erect, in which case appendages take care of the spore orientation or if the sporogenous portion is unobstructed at the surface it need produce only sterigmata.

As would be expected, there is considerable variation in the morphology of the basidium and its parts. The lateral hypobasidium or "sac," the most conspicuous feature of the fructification, is typically oblong-ovoid, but often it is constricted once or more (fig. 18a, b), a condition culminating perhaps in the extremes illustrated by *f* and *g* of the same figure. It should be noted that the general orientation of the fructification is such that the hypobasidia are only rarely pendent as extant accounts say. The fructification is resupinate, commonly effused on the under side of logs, hence the general configuration is to be construed inversely to the usual interpretation (fig. 19). Usually the epibasidium originates from a terminal primordial cell as a vertical outgrowth from it, but occasionally it seems to have

been produced directly from the proximal end of the hypobasidium. The latter situation would then be equivalent to what apparently is the rule rather than the exception in *H. intermedia*. After examining Linder's material and his illustrations it is quite clear that there is a real difference in the origin of the basidial components of these two species. In *H. Lagerheimi* those hypobasidia which seemingly are not borne on terminal primordia with subsequent elongation of the epibasidia, but which appear to produce their epibasidia directly at their proximal end, are in reality borne on primordia which are short lateral branches of a proliferating complex. Hence their true origin is from a single terminal cell from which the hypobasidium arises in the ordinary fashion. This is clearly substantiated by the position of the walls (cf. figs. 21a, b; 75a, b). In *H. intermedia* one can easily trace the origin of the saccate type of hypobasidium from an intercalary binucleate cell which pushes out the hypobasidium, just as in *H. Lagerheimi*, and it in turn produces proximally the epibasidium (fig. 75b, c, d). There is, then, a fundamental difference between these two species in regard to the position and origin of the basidium and its components. In either species the type of development characteristic for one may occur as a rare exception in the other. Whether the primordium be terminal or intercalary, it is always distinguishable by its denser protoplasmic content. A study of *H. caroliniana*, *H. Lagerheimi*, and *H. graminicola* reveals that they are essentially identical at these stages. A third variation occurs in *H. pinicola*. Here the primordium is intercalary, but the epibasidium originates with a lateral outpushing of the primordium, usually more or less apical, rather than from the proximal germination of the hypobasidium (fig. 72b, c). No case of distal germination of the hypobasidium, such as Linder reported in his work, has been noticed in any of the material examined.

Quite early the budding epibasidium is visible at the apical end of the primordium. It is seldom distinguishable before the latter attains its mature diameter or previous to the formation of the hypobasidium, and it may not appear until much

later (cf. figs. 5, 22, 31b). Exceptionally, it is lateral in position. Its further development is either upright or variously bent, consequent upon its origin or the requirements for spore discharge (fig. 23). If there is a constriction between primordium and epibasidium it persists and is apparent in all stages, though there are numerous instances in which the epibasidium is little, if at all, distinct from the primordial portion (fig. 25b). The elongation of the epibasidium is various in relation to the accompanying nuclear behavior. It may follow one of three general patterns: I, The nucleus migrates from the hypobasidium as the epibasidium elongates (fig. 24); II, The elongation of the epibasidium distinctly precedes the nuclear migration (fig. 25a, b) which may be delayed until a stage as late as that shown in figure 10; III, Migration precedes elongation. In such event there is little if any protoplasmic evacuation of the hypobasidium until the epibasidium begins elongating (fig. 26a). The last scheme is infrequent except in less well developed fructifications. This results in a distinctly shorter basidium whose developmental sequence may be followed in figure 26b, c, d, and e. The other two types occur about equally, though type I probably represents the typical behavior. Type II seems more often associated with an extremely long unconstricted form of epibasidium and is undoubtedly a direct response to its location within the fructification. Types I and II intergrade. The type of behavior is consequent upon the primordium location. In general, if the primordium is near the surface there is no need for great elongation, but if it is well within the fructification the longer form necessarily results.

The crimp at the base of the epibasidium, though persistent, is never cut off by a wall. However, a second constriction is located characteristically just below the inflated sporogenous part. Such a joint has been noted by Coker in *H. caroliniana*; Wakefield and Pearson ('23) and Rogers ('34) show it in different degrees for *H. Lagerheimi*. According to Wakefield and Pearson there is no wall at this point; according to Rogers there is. Rogers' figures present a condition comparable to the one Coker noticed. In *H. Lagerheimi* three septa are found

more frequently than four in the sporogenous portion. Commonly, protoplasmic remnants simulate a basal wall, but the actual presence of a wall is exceptional (fig. 58). Ordinarily, the second constriction lies just behind the evacuation level of the fourth segment (figs. 12, 13, etc.); it may be accompanied by a bend. At times the constriction is very deep, and if in addition the fourth segment has a basal septum, the condition is identical with Rogers' illustration (fig. 27a, b). Whether the last segment does or does not have a basal wall, there is never any protoplasm left behind the segmented portion. In *H. caroliniana* the fourth septum is evident early in the development of the sporogenous portion (fig. 76b). Again the articulation receives varying emphasis so that one finds examples ranging from a definite joint, as Coker showed, to a simple bend.

CYTOLOGICAL OBSERVATIONS

Each hyphal cell characteristically contains two small nuclei whose position within the cell is various. The origin of the two-nucleate condition was not determined. As the cells grow older and elongate their protoplasmic content is much reduced until it may consist only of scant bits around the nuclei. The nuclei of the hyphae, however, remain small. Each nucleus is composed of a deeply staining central nucleolus embedded in the homogeneous nucleoplasm and is surrounded by a delicate membrane which is barely differentiated from the cytoplasm in which the whole lies. The apical cells destined to become the basidial primordia are limited to the more actively growing regions near the surface of the fructification. Their contents more nearly fill the cell and stain as an even, homogeneous mass. Consequently these primordia and the sub-adjacent cells are the most favorable places to locate mitosis. This is typically conjugate, both nuclei being entirely synchronized in behavior, though the smallness of the cells and of the nuclei at this stage makes detailed analysis practically impossible. At times one finds the spindles in the well-known side-by-side orientation or slightly oblique (fig. 28a). Curiously enough, in by far the

majority of cases the figures are crossed at varying angles (fig. 28b, c). Future orientation of the spindles in this way is implied clearly in the early stages shown by *a*, *b*, and *c* of figure 29. Such behavior is probably due to the small diameter of the cell which would prohibit a side-by-side arrangement. No additional details could be discerned except that the membrane has disappeared by the time of spindle formation, and sometimes the remnants of the nucleoli are visible in the nuclear cavity. Later they disappear (fig. 30). Following mitosis a wall is laid down between the two daughter dikaryons. This process may continue for several divisions but eventually the terminal cell constitutes the future primordium. The wall may not be formed immediately. In figure 31a, where it has just been laid down, the nuclei give evidence of a longer reorganization. Here, too, the cell contents are quite vacuolate, the result probably of rapid elongation and growth. The nuclei of the primordium are in a typical resting condition.

When first delimited the primordium is little distinguished in size from the hyphal cells. Before the production of the hypobasidium it increases in diameter and somewhat in length, though again it is difficult to evaluate this exactly in a form so variable in size and behavior. Examples in figure 32 represent an increase with reasonable surety, for they were approximately adjacent in the same section.

Beginning as a lateral outgrowth of the primordial cell just anterior to the basal septum, the hypobasidium rapidly assumes the form of an inflated sac-like appendage (figs. 31b, 33). At no time in its development is it without cytoplasm. As the hypobasidium elongates the nuclei in the primordium, which up to now have been more or less centrally located, enlarge slightly and prepare to move into the hypobasidium. They are now somewhat ellipsoidal. Sometimes the nuclei lie in such close association that they seem to be fusing, but careful focusing reveals that their individual membranes are intact (fig. 34a, b). One nucleus of the pair may precede the other into the hypobasidium by a considerable distance (fig. 35). In any event, the movement is always tandem, with the long axes

of the nuclei parallel to that of the primordium. There is no change in their shape as the nuclei pass through the narrow neck connecting hypobasidium and primordium. Following this migration the primordium is commonly more vacuolate (fig. 34b). Darker staining masses in the protoplasm are suggestive of a protoplasmic flow accompanying the nuclear passage (figs. 35, 37). Occasionally one nucleus of the pair may be larger, but this only signifies an earlier increase in its volume (fig. 38d, e). Once in the hypobasidium, the nuclei come together for fusion. Up to this time the hypobasidium has been growing but after karyogamy growth ceases. The two nuclei ordinarily do not penetrate below the mid-region of the hypobasidium, except in the case of the constricted hypobasidia where they always lie in the larger portion (fig. 18a, b, f, g). At the point of contact their membranes break down, allowing the components of the two nuclei to intermingle completely (fig. 38c). Usually until then their structure is no more differentiated than in the resting stage, although in figure 38d one nucleus is already forming a reticulum. A little later the fusion nucleus is dumb-bell-shaped but this constriction is transitory (fig. 39). The fusion nucleus is bounded by a continuous membrane; it contains two nucleoli, usually opposite each other, and a reticulum in varying degrees of advancement. The few variations of these earlier stages involve only minor deviations from the pattern. First, there is variability in the position of the nuclei in the hypobasidium. Figure 38e illustrates deeper penetration than usual. Another difference is that at times one nucleus is somewhat more advanced, as evidenced by its greater volume and earlier appearance of a reticulum (fig. 38e). In general these variations are rare, the migration and fusion processes being quite regular.

Within the fusion nucleus, now spherical in outline, the nucleoli draw together to unite (fig. 40a, b, c). The single resultant nucleolus clearly has an increased volume. By now the nucleus has very nearly attained its maximum size, with a diameter as much as five times that of the nuclei when in the primordium, almost equivalent to that of the hypobasidium.

Simultaneously the nuclear content is undergoing change. A sharp reticulum or network of threads develops throughout, highly suggestive of mitotic prophase. This increases in complexity until it reaches a stage illustrated in figure 41a. As the threads thicken, distinct, deeply staining beads representing aggregations of chromatic material are scattered throughout on them (fig. 41b). From this point on the nucleus is contracting and its entire contents become more concentrated and uniformly deeply staining. The single nucleolus gradually shifts from an eccentric to a centric position. This contraction is preliminary to a resting stage which will be followed by nuclear migration from the hypobasidium through the primordium to the epibasidium (fig. 42a, b). This contracting or post-fusion stage is the one most commonly seen; hence it probably involves a considerable span of time. With its contraction the nucleus becomes more and more homogeneous until it resumes the typical resting condition. When completely contracted the nucleus has a total volume not much in excess of the unfused nuclei at the time of migration but the nucleolar material quite evidently has been doubled in volume (see figure 71 for comparative nuclear and nucleolar ratios). The fusion nucleus ordinarily is in the center of the typical hypobasidium; in the constricted type it lies in the largest portion.

With the return to the resting condition the nucleus is ready to leave the hypobasidium. The primordial cell in the meantime has given rise to the epibasidium, more or less greatly developed. If the migrating nucleus is at all elongate the whole body moves with its long axis parallel to that of the hypobasidium, later to those of the primordium and epibasidium (fig. 43a, b, c). As in the earlier migration, there is no attenuation or change of form when the nucleus passes through the neck, for the diameter of the migrating nucleus never exceeds that of the neck. When the nucleus leaves the hypobasidium the protoplasm also withdraws, leaving the distal portion first, until the hypobasidium is completely emptied and withers. Evacuation eventually extends to the primordium and lower

portions of the epibasidium as their contents are withdrawn to augment the expanding sporogenous portion.

The epibasidial development at this time follows one of the plans already outlined. Of these the first two are by far the most common. In accord with these types, I and II, the first evidence for nuclear division is the enlargement of the nucleus followed by the appearance of threads in the heretofore homogeneous structure. This may begin at a level as early as that represented by figure 44b, but typically there are no signs of division until the nucleus comes to lie in the enlarged portion of the epibasidium, the actual sporogenous part (fig. 45a). By now all the protoplasm has withdrawn from the rest of the basidium into that region. There is seldom any further elongation or increase in diameter of the latter once division stages have been inaugurated. This first division of the secondary nucleus is taken to be meiotic. Once again the nucleus increases in volume, often nearly equalling the diameter of the tube, usually much elongated, in general conformable to the space in which it lies (figs. 46, 49). An increase in volume is the first diagnostic sign of the prophase and is the more marked because of the lighter staining properties of the nucleoplasm. This is followed by the gradual appearance of threads which soon become definitely organized. The membrane is intact about the threads and nucleolus. Chromatic beads appear on the threads but they are never as pronounced as those seen in the fusion nucleus (fig. 47). The threads thicken, become denser, and frequently are localized at a pole opposite to the nucleolus, even from the beginning (fig. 48a, b). The nucleolus is usually peripheral, rarely central. Stages represented in figure 48 may be interpreted as synaptic. Following this, the chromatic material is increasingly concentrated until it is massed more or less centrally in the nuclear cavity (fig. 48c). Slightly later, individual clumps are distinguishable in the mass and probably represent pairs or groups of chromosomes. The nucleolus, as yet distinct, from this point onwards decreases in size and finally disappears. No clear-cut evidence

was found for its direct expulsion into the cytoplasm. It usually is pushed to the edge of the nucleus quite early, and when the membrane breaks down lies free in the cavity or near by in the cytoplasm. Rarely is it distinct when the spindle is delimited; in one exceptional case a nucleolus was still quite sharp at anaphase. Commonly, what has been interpreted as a last remnant of it is seen in the cytoplasm (figs. 50b; 51a, b).

Development in accordance with type III must be considered a special case. There the prophase is distinct quite early in the development of the sporogenous portion, at times when the latter is just differentiated (fig. 45c) or even earlier. The nucleus here is less drawn out because it lies in a broader area. Aside from the earlier initiation point there is no further variation in procedure. The whole is simply a shortened basidium whose developmental processes as a consequence are likewise foreshortened.

A metaphase of the sort found in the higher plants has not been seen. As the chromatin mass separates into individual units, presumably chromosomes, a spindle is formed intranuclearly. It is always oriented parallel to the long axis, never oblique. Because of the extremely small figure, spindle fibers are not distinguishable, but the whole region appears simply as a darker-staining area. At the poles there are minute but definite dark-staining bodies, the centrosomes—more properly centrioles, for no further differentiation can be made. Their origin is unknown. Astral radiations do not occur. As the chromosomes pass into anaphase the nuclear membrane disappears, leaving the division figure in the nuclear cavity (fig. 50b, c, d, e).

At anaphase the chromosomes pass to the poles in a very irregular manner, for they may be so scattered in their distribution as to extend from equator to poles (fig. 50). It is during this scattering, if ever, that one can count the number of chromosomes present. The size of the figure and its chromosomes precludes any finality of count. As nearly as can be determined there are at least five pairs of chromosomes of different sizes.

Even though the membrane has broken down, the nuclear cavity, by virtue of its lighter staining properties, remains distinct for much longer, as figure 51c, a late anaphase, illustrates. There the spindle is stretched out and lengthened: the chromosomes are no longer discernible as individual units, for the majority are already massed together at the poles. There is no longer any trace of a nucleolus. The polar massing and the lengthening of the spindle continue until at telophase a condition represented by figure 52 is characteristic. The connective fibers or strands between the two polar masses are conspicuous. Similar persistent strands have been noted in the fungi by numerous authors. Tischler ('21-'22) designates them "karyodesmotische," Bensaude ('18), "pont cinoplasmique," and Colley ('18), "suspension fibers." That their occurrence is far from uncommon is evident from the frequency of reports covering a wide distribution of forms (cf. Blackman, '04, Colley, '18, Lindfors, '24, and Pady, '34, on rusts; Maire, '08, on divers basidiomycetes; Neuhoff, '24, on the secondary nuclei of Auriculariaceae and Tremellaceae). These connections are still distinct when lighter areas around the now almost structureless chromatic masses give clear indication of the reorganizing daughter nuclei (fig. 52). Gradually a delicate membrane surrounds them. Apparently the chromatic masses prominent at telophase become the nucleoli of the daughter nuclei, a situation commented upon by Sass ('29) in his studies of Agaricaceae.

The two nuclei are usually synchronized in their behavior but now and then one matures in advance of the other (fig. 56a, b, c). A wall separating the two nuclei either is laid down before reorganization or much later. It is distinguishable at first only as a very delicate deposition, barely differentiated from the surrounding protoplasm; occasionally a clearer zone seems to mark its future position. Delay of the wall formation until the nuclei are undergoing the second division is the exception (fig. 56b). As nearly as could be determined the wall is formed by uniform deposition. Frequently a heavier aggrega-

tion is made out mid-way on the spindle strands. This may represent the initiation of the new wall (figs. 52d, 56b).

Daughter nuclei from the first division never reach a particularly high degree of reorganization, for the second division follows almost immediately. That this does ensue rapidly is inferred by the fact that early-division stages of it were never seen. Spindle orientation is longitudinal, with only an occasional and minor deviation to the oblique. Anaphases with characteristic spindles and darker-staining bodies, the chromosomes, are common (fig. 55). In figure 56a the nucleolus of one dividing nucleus has been cast aside and is disintegrating. The subsequent behavior resembles that of the first-division figures and leads to the formation of four nuclei. Moreover, the spindles are notably smaller than those of the previous division and therefore the chromosome number could not be determined with any degree of satisfaction. An exactly parallel situation has recently been recorded by Pady ('35) for the division of the fusion nucleus in the promycelium of *Hyalopsora*. Ordinarily the two nuclei progress at equal rates, but when they are not synchronous the basal segment may have a nuclear phase as advanced as late telophase while the upper is still in anaphase, or vice versa (fig. 56a). Again a spindle may not have formed in one, although the second is already in anaphase. When all four nuclei are reorganized there results the typical segmented spore-bearing part (fig. 57). In that figure the mid-wall, the first one formed, is clearly older and better developed; the other two have just been laid down. As already noted, a fourth septum is exceptional, but if present it appears later at the base of the fourth segment. Figure 58a shows a true septum but figure 58b illustrates how protoplasmic remnants may simulate it.

The four daughter nuclei often display an inequality of size, that of the basal segment being subject to the greatest variation, for it is often noticeably smaller than the others. These nuclei are all in a resting condition. Though their total volume now is slightly greater than in resting nuclei elsewhere, the nucleolus is no longer enlarged. Here, if ever, two nucleoli

may appear, though apparently the condition is evanescent (fig. 59). This is in accordance with the already ascertained fact that nuclei may show variability in this respect, especially after several successive divisions, such as is the case here (Sharp, '34). That there is great variability in the nuclear and nucleolar volumes all through the cycle is evident (fig. 71).

Sterigmata promptly appear as small outgrowths from each segment (fig. 60). They are not formed synchronously nor in any regular order of succession. In most instances the fourth segment is the last to produce its sterigma, but it may be the first segment in which production is longest delayed. Initiation commonly starts in the second unit (fig. 61). There is no correlation between the position of the hypobasidium and the side of the sporogenous portion which produces the spores, but the spores are borne on the convex side. Sometimes the end segment bears its sterigma apically (fig. 63a); infrequently sterigmata may be borne on opposing sides (fig. 63d). At this time the nuclei are usually to be found directly opposite the budding sterigmata, more often peripheral than central. Gradually the sterigmata lengthen, and then small vesicles, the future spores, appear at their apices (fig. 62).

Sometimes the vesicle is preceded by a dark-staining cap or plug whose nature was not determined (fig. 64a, b). Colson ('35) finds a similar condition during early sterigmatic production in *Psalliota campestris*, where a small quantity of stainable material appears in the narrowest region. She considers it merely a mechanical retention of stain. Such would also seem to be the case here. Only the initial spore stages are hyaline, and the expanding spore is henceforth never without a definite protoplasmic content. Protoplasmic migration from the basidium segments begins early and precedes nuclear migration, which does not take place until the spore is practically mature. The latter induces striking changes in the nucleus. While the spore is forming the nucleus becomes decidedly more stainable and completely altered in shape (fig. 65a-d). Finally it becomes very dense, staining homogeneously black, and by then is quite elongate and more or less irregular in outline. It

moves into the sterigma as an undifferentiated compact mass (fig. 66a, b). Often it is long and slender during its progress into the spore (fig. 66c, d). This is not an uncommon phenomenon in the basidiomycetes. As the nuclear mass penetrates the spore the latter may show vacuolation. By now the protoplasm is well withdrawn from the segment, the last remnants passing in with, or just after, the nucleus. No protoplasmic lining ever remains in the cells as Buller ('22) noted in the Auricularieae. Once within the spore the nucleus undergoes corresponding changes in reverse order until the true resting nuclear state is again attained (fig. 66e, f, g, h, i). The volume is slightly under that of the antecedent resting condition.

In discussing the general morphology, the formation of exceedingly long thickened appendages in place of sterigmata was touched upon. At first it was thought that these might be indicative of direct germination as the nucleus early moved into them without undergoing change. But later it was found that they result directly from the position of the basidium and are merely a means of elevating the spores to the surface. Their consistent occurrence in regions of greater compactness in the fructification bear this out. Sometimes the lower segments of a basidium have these appendages, whereas the upper one produces an ordinary sterigma (fig. 63a). Eventually the appendages produce true sterigmata and spores, terminally. This procedure is well known in other heterobasidiomycetes; for example, in *Auricularia* the long appendages push through the gelatinous matrix to bring the sterigmata and spores to the surface. In the rusts normally (Gäumann and Dodge, *l. c.*) as well as under unfavorable conditions, the basidiospores are produced only when brought to the surface. The nuclei then move into the spores, having undergone the changes described. These nuclear changes may begin early, the initiation point being correlated with the length of the appendage (fig. 67e, f). The nuclear behavior is in complete agreement with Neuhoff's criterion for a sterigma. Linder speaks of variation in sterigmatic length in *H. intermedia* (see his pl. 41, figs. 13-15), a situation which is probably tantamount to the one just described.

Germination, which may take place at once, begins with the emission of a short germ tube and a sterigma upon which a secondary spore exactly like the first is borne (fig. 68b, c, d). This is the so-called "germination by repetition," long a recognized character of the heterobasidiomycetes (Patouillard, '87). Not only is the morphology of the sterigma the same but the nucleus, in order to pass into the secondary spore, is altered in exactly the same fashion as characterizes the passage from basidial segment to spore (fig. 69). Nuclear division within the spore has never been seen. At times spores begin germinating while still attached to the sterigmata (fig. 68b). No data pertaining to the actual spore discharge were obtained.

Attempts to culture *H. Lagerheimi* have been unsuccessful so far. Unfortunately no fresh material was available, and herbarium specimens of the 1934 collections had to be relied upon. Spores from that source sown in hanging-drop cultures of sterile distilled water gave a goodly percentage of germination within from 24 to 48 hours, but transfers were never successful. From observation of spore behavior in the hanging-drop cultures it is readily seen that the usual mode of germination is by repetition. Möller illustrates septate spores, each segment of which is capable of producing a secondary spore. This has not been seen. Although in Patouillard's type material a spore with two germ tubes was found, septation between was indistinct. The spores do occasionally segment in germination, but their subsequent behavior was not determined. Small sub-globose conidia appear in older cultures. Their mode of origin was not seen. Frequently they are massed, just as Möller reported.

Before the appearance of the germ tubes the spores are quite hyaline, in most cases with a single, rather conspicuous oil globule. As germination processes are initiated this divides into two to many with corresponding reduction in size. When the germ tube arises the contents of the spores are distinctly granular with numerous oil bodies. The tubes themselves are mostly lateral, but may be terminal, in position. At their apices a small bubble-like protuberance is the first sign of the

secondary spore. This remains quite hyaline until maturity when the content of the original spore is discharged into it. In some cultures within a few days delicate mycelial outgrowths were evident (fig. 70).

TAXONOMIC CONSIDERATIONS

All the species of *Helicogloea* are entirely saprobic. They are found on well-decayed woods of various kinds, including pine, alder, birch, beech, oak, aspen, poplar, and willow, rarely on humus or soil. One species occurs on grasses from whence it takes its name, *H. graminicola*. Collections have been made of some species practically throughout the year; others seem to have more seasonal limitations. Any is more likely to be found in damp rather than dry weather. Geographically, the distribution is scattered. *H. Lagerheimi* is the most widespread. Besides the type locality, Ecuador, it has been reported from France, England, and the United States. The only other North American species are *H. caroliniana*, as yet found only in the type locality, North Carolina, and *H. pinicola* recently reported from Canada.

As pointed out earlier, the chief considerations of the genus have been taxonomic. The most comprehensive treatment is that of Bourdot and Galzin. They characterize the genus as "floccose or gelatinous-mucous, spreading; the probasidium in the form of a sac, laterally pendent and giving rise to a basidium with three transverse walls; sterigmata lateral (one terminal); spores hyaline, smooth." By reason of the floccose or gelatinous nature of the parent genus, these authors have erected the subgenus *Saccogloea* to care for the mucose-gelatinous forms. Furthermore, they comment: "The French species of *Saccoblastia* do not always show the generic characters clearly; the contents of certain probasidia appear often to be a reserve utilized for the formation of the basidium, but it seems in many cases that it is the probasidium itself which becomes erect and is directly transformed into a basidium. At least, the section shows often all the intermediate stages between the probasidium as a pendent sac and the curved or erect

ERRATA

Substitute the accompanying plate 11 for that published in Baker's "A Study of the Genus *Helicogloea*" in Ann. Mo. Bot. Gard. **23**: *pl. 11*. The following list of errata is also for Baker's paper.

p. 89: under *H. pinicola* read—Pl. 12, figs. 72 a-l, 73 a-e.

p. 92: under *H. caroliniana* read—Pl. 13, figs. 76 a-e.

p. 97: first sentence, second paragraph, insert *no*—From the table following it is clear that there is *no* . . .

p. 124: the explanation of plate 12 should include figs. 72 and 73, now on p. 126.

basidium.” In view of such indefiniteness all obtainable species were studied. A brief description is given of each, chiefly for its morphology.

HELICOGLOEA pinicola (Bourd. & Galz.), comb. nov.

Pl. 13, figs. 72a-l, 73a-c.

Saccoblastia pinicola Bourdot & Galzin, Soc. Myc. Fr.
Bull. 25: 16. 1909.

The type has not been seen, but two collections of Galzin's, and Bisby's Canadian gathering were examined. They are all truly floccose. The scattered receptacles of Galzin's collections are Cartridge-Buff.² A few patches here and there, gelatinous in consistency, are a deeper color—Olive-Buff to Deep Olive-Buff. The Canadian material shows no gelatinous areas.

This species is clearly a member of the floccose section. Bourdot's and Galzin's description answers with some exceptions. The hypobasidium was found to be consistently larger than the range given by these authors. They say it is $40-45 \times 8-12 \mu$; measures made here extend the range to $19-56 \times 7-14 \mu$, the majority in Galzin's material falling around 50μ in length. The morphological plan is even less in agreement. Bourdot and Galzin refer to variation in the “basidia” but not to any in the hypobasidia. In the material studied the latter is extremely noticeable. Irregularities most frequently take the form of forked or branching hypobasidia (fig. 72a, i, j). Forked basidia mentioned and figured by Bourdot and Galzin have not been found, but figure 72i, for example, strongly suggests that these authors may have mistaken forked hypobasidia for forked basidia. The most striking feature is the mode of origin of the basidium parts. Occasionally the primordium is a terminal cell of varying length, as in *H. Lagerheimi*, but usually it is intercalary. The hypobasidium arises in the usual way as a lateral outgrowth but at maturity presents a great variety of forms—from straight to constricted to forked (fig. 72). The size is usually great in comparison with those of other species. The epibasidium is produced as a lateral

² Capitalized color names are from Ridgway, R., Color Standards and Color Nomenclature. 1912.

out-pushing of the primordium at or near its apex. Hence one commonly finds the basidia appearing in chains in contrast to the type of proliferation common in *H. Lagerheimi* (fig. 73e). At maturity the spore-bearing region of the epibasidium is three- or four-septate, and the portion posterior to it withers. Apical germination of the terminal segment is common (fig. 72e, k).

Bourdot and Galzin say this species is "very close to *H. graminicola*, of which it is perhaps only a variety. It differs in habit and the basidia and spores are notably larger." There seems to be little basis for the assumption of varietal status. True, both species have conspicuous clamp connections and both are supposedly floccose, but the epibasidial character and origin in the two are entirely different, nor does *H. graminicola* ever show the hypobasidial irregularities so marked in *H. pinicola*.

A collection from Litschauer of this species on *Alnus viridis* undoubtedly belongs to the form *alniviridis*, although it was approved by Bourdot before he segregated the form. It shows no deviation from described characters except that there was no paucity of hypobasidia such as Bourdot reported. Morphologically it is identical with the species (fig. 73 a-e). The validity of forms founded on substratal attachment is questionable for pure saprobes, even more so in this case since the advent of Bisby's specimen which was found on *Populus*. It, too, showed no specific differences.

FRANCE: Causse Noir, April 25, 1910, *Galzin*, 20555 (in Herb. Univ. N. Car. ex Herb. Bourdot); Nov. 19, 1916, *Galzin*, 2104 (in Farlow Herb. ex Herb. Burt).

AUSTRIA: Tirol, Aug. 15, 1924, *Litschauer* (in Herb. Univ. Iowa).

CANADA: Manitoba, Victoria Beach, Aug. 23, 1935, *Bisby*, F5695.

HELICOGLOEA graminicola (Bres.), comb. nov.

Pl. 13, figs. 74a-d.

Saccoblastia graminicola Bresadola, Ann. Myc. 1: 112.
1903.

After this is moistened it appears as a thin gelatinous coating on a grass stem, in color Vinaceous-Buff. There is nothing in its structure or consistency to justify Bresadola's

adjective "tomentose." From phloxine-stained mounts one can readily distinguish its salient characters. Micro-dimensions show close correspondence to those given by Bresadola. The primordium is terminal and it gives rise to the epibasidium. A conspicuously elongate connection between primordium and sporogenous portion is not found. The hypobasidia are large, coarser in appearance than those of *H. Lagerheimi*, more constant in size than those of *H. pinicola*, and are never forked. All the protoplasm withdraws from the hypobasidium but not necessarily from the primordium, which may still show a definite protoplasmic content after the segmentation of the spore-bearing region (fig. 74c). Clamp connections are prominent on the hyphae, sometimes appearing on the basal septum of the primordium which just beyond on the opposite side is producing the hypobasidium (fig. 74a).

Eichler (in Farlow Herb. ex Herb. Bresadola, ex Herb. Patouillard).

HELICOGLOEA intermedia (Linder), comb. nov.

Pl. 13, figs. 75a-h.

Saccoblastia intermedia Linder, Ann. Mo. Bot. Gard.
16: 488. 1929.

A slide of the type material prepared by Linder was studied for the morphology of the species. From this it was clear that the origin of the saccate hypobasidium is intercalary, not terminal, or only exceptionally so. Following nuclear fusion within the hypobasidium, the latter germinates proximally to the epibasidium. After great elongation four sterigmata and spores are formed on the thickened end. Linder uses the terms "probasidium, promycelium, and basidium" for these parts. However, there is no reason, in spite of morphological variation, why Neuhoﬀ's terminology is not applicable. The clavate type simply represents direct development from a terminal primordium. In this event, when a lateral sac is not produced, fusion takes place in the clavate portion itself; hence it is to be interpreted as the hypobasidium and its subsequent outgrowth as the epibasidium. Figure 75 is included merely for comparison with the other species.

Linder speaks of the saccate hypobasidium exhibiting distal germination at times. If his figures (pl. 40, fig. 4; pl. 41, fig. 9) represent the best evidence for that phenomenon, its occurrence is questionable. Succeeding stages would be convincing but none was found. However, the hypobasidia are frequently constricted, once or more, and it is possible that this so-called distal germination is only an extreme constriction. Distal germination was never seen in *H. Lagerheimi*. Hypobasidia of the form illustrated in figure 75e, *H. intermedia*, might be interpreted as unusually constricted, especially when compared with figure 18f and g of *H. Lagerheimi* which is so construed. Furthermore, if the orientation of the two fructifications is the same, then distal germination could only occur for those rare cases where the hypobasidia are lateral or pendent.

CUBA: Soledad, Sept., 1924, *Linder*, TYPE (in Herb. Mo. Bot. Gard.).

HELICOGLOEA caroliniana (Coker), comb. nov.

Pl. 13, figs. 76a-c.

Saccoblastia caroliniana Coker, Jour. Elisha Mitchell Sci. Soc. **43**: 233. 1928; *S. ovispora* Möller var. *caroliniana* Coker, Jour. Elisha Mitchell Sci. Soc. **35**: 121. 1920.

Coker's descriptions are so adequate that little need be said here. The fructification is a particularly well-developed gelatinous one. In its morphological behavior it resembles *H. Lagerheimi* very closely. A series of diagrams is included for comparison. Here, as in the other species of the genus, long appendages may precede the formation of sterigmata and spores (fig. 76d).

NORTH CAROLINA: Chapel Hill, April 15, 1920, *Couch*, 4256 (in Herb. Univ. N. Car.); Chapel Hill, July 31, 1920, *Couch*, 4601 (in Herb. Univ. N. Car.).

HELICOGLOEA LAGERHEIMI Patouillard, Soc. Myc. Fr. Bull. **8**: 121. 1892. Pls. 7-12; pl. 13, figs. 77-78; pl. 14.

Saccoblastia ovispora Möller, Protobasidiomyceten, Bot. Mitt. **8**: 16. 1895.

Saccoblastia sebacea Bourdot & Galzin, Soc. Myc. Fr. Bull. **25**: 15. 1909.

Saccoblastia sebacea var. *vulgaris* Bourdot & Galzin,
Hym. de France, p. 5. 1928.

Saccoblastia sebacea var. *pruinosa* Bourdot & Galzin,
Hym. de France, p. 5, 1928.

A study of the type material resulted in the above changes in synonymy. Figures 79–81 show the development of the basidium as seen in Patouillard's material, from the initiation of the primordium to the mature basidium and spores. Though micro-dimensions are consistently larger than those from the majority of collections, they do not exceed the uppermost figures obtained. There is no uncertainty about the identity of this material with Möller's or Bourdot's and Galzin's. Therefore the earliest name takes precedence. On the basis of basidium size *H. caroliniana* is perhaps the nearest species. But the two are so totally different in their habit they could never be confused. In particular, the hypobasidia of the type collection are sometimes constricted and frequently are set farther forward in relation to the basal wall of the primordium (fig. 79d) than usual. No case of intercalary origin was noted in this material.

Saccoblastia sebacea B. & G., an acknowledged gelatinous form, has been separated from *S. ovispora* Möller largely because the latter was supposedly floccose or hypochnoid. A study of all available specimens and descriptions has been made in an effort to straighten out the situation.

Of *Helicogloea Lagerheimi* (*Saccoblastia ovispora* Möll.), Möller wrote: "Sie bildete einen dünnen, fast durchsichtigen lockeren weissen Ueberzug, der in ganz unregelmässiger Umgrenzung mehrere Centimeter in jeder Richtung sich ausdehnte. Bei sehr feuchtem Wetter sieht dieser Ueberzug fast schleimig aus, da das Gewirr der Fäden Wasser zwischen sich festhält, bei trocknerem Wetter dagegen bemerkt man nur einen lockeren Hyphenfilz, der bei vollständigem Trocknen zur Unsichtbarkeit zusammenfällt." (l. c.). Ferry ('96) the following year translated Möller's work into French, in addition utilizing Möller's plates. The structure of the fructification is described as irregular patches of white loosely interwoven hyphae. Lindau ('97) introduced the adjective "wer-

gartig'' in his characterization. As yet only Möller's species were known. Patouillard ('00) delineated the genus *Saccoblastia* as floccose, soft, and said of the tribe Septobasidiés to which he assigned it: "Floconneux ou crustacé, non gélatineux." Chronologically Bresadola's ('03) report is next, which described *H. graminicola* as "tomentose." Clements ('09) placed the genus (as *Saccoblastia*) in that group of Auriculariae having a byssoid pileus. Clements and Shear ('31) adhere to this characterization. Saccardo ('82) qualified the structure by saying, "Est quasi *Hypochnus* sporis pleurogenis." Killerman ('28) repeated Lindau's diagnosis for two species, having replaced *H. sphaerospora* with *H. graminicola*. The character of floccose as opposed to gelatinous is the distinguishing one for two sub-genera in Bourdot and Galzin.

Thus there had gradually crept into the literature the conception of floccose or hypochnoid fructifications in *Helicogloea*. *H. pinicola* is truly floccose. The interpretation of *H. Lagerheimi* as floccose probably has been considerably strengthened by Bresadola's comment to Coker in reference to *H. caroliniana* which was first described as a variety of *H. Lagerheimi*. Coker says (*l. c.*): "I later sent some to Bresadola who has described a sp. of *Saccoblastia* and seems to have seen *S. ovispora*. He writes as follows: 'For me it is a species quite distinct from *S. ovispora*. The genus *Saccoblastia* is not gelatinous; your species is gelatinous like *Platygloea*; . . .'"

An exactly parallel situation has arisen in the case of *Stypella minor* Möller and *Tremella gangliformis* Linder. As Martin ('34) points out, the error is not in Möller's original description but in subsequent misplaced emphasis and consequent distortion. Since the type of *Helicogloea Lagerheimi* is mucous-gelatinous, all necessity of maintaining these species separately is removed. Unfortunately, Möller's type specimen has not been located; Rick's material, agreeing well with Möller's descriptions and coming from an adjacent province, gives strong likelihood of being the same fungus. The type of Bourdot's and Galzin's species likewise has not been seen, but all the collections so labelled which have been at

hand were decidedly not floccose. When any of these specimens is moistened it is mucous-gelatinous, but as it dries one can trace just such a sequence as Möller described.

Throughout the genus there seems to be not only inconsistency of interpretation but a real variation in the nature of the fructification itself. Wakefield and Pearson ('23) note of *H. Lagerheimi* that a series of specimens shows the "mucous-gelatinous" texture only in later stages. "When at its best the fungus has somewhat the consistency of *Corticium confluens*, and is beautifully pruinose with the projecting basidia and spores." Rick (personal correspondence, 1934) says: "The *Saccoblastias* are surely hypochnoid without true hymenium, but when well developed they are gelatinous, like *Exidiopsis*, and dry a little glancing." To Rick obviously hypochnoid connotes structure rather than consistency. On that basis all the species are "hypochnoid." It is significant that he considers the genus gelatinous, even though earlier he had been in accord with conventional treatments when in a monograph of protobasidiomycetes ('33) he referred the genus to the floccose Auriculariales. As already remarked, *H. pinicola*, which is distinctly tomentose for the most part, has some scattered gelatinous patches.

Möller's statements may have left latitude for differing interpretations, but his figures are clear-cut and easily show the close resemblance to *H. Lagerheimi*. A table of measurements for the specimens under discussion shows there is no reason to maintain any as distinct species because of variation in size. Only in the event that Möller's type proved to be distinctly floccose would it be reasonable to retain that species.

Two collections from Brazil were studied, both Rick's. The first of these was quite inconspicuous until moistened, when it became visible as thin gelatinous film, faintly pustular, of a Buffy-Brown color; no part of it could be interpreted as floccose. Unfortunately, the specimen was so contaminated with hyphomycetes that mounts were far from satisfactory, the more so as it did not seem to be in a particularly advanced fruiting condition. However, all evidences indicated a struc-

tural development much like the type of *H. Lagerheimi*. The mycelium is typical; oblong-ovoid hypobasidia—straight or constricted—are borne laterally on terminal primordia (fig. 78a). There is rarely deviation from the typical epibasidial production (fig. 78e).

The second of the collections may easily be a portion of the first, to judge from appearances. Certainly when examined before moistening it is not at all floccose. If discernible at all when dry it is only as a dried mucoid layer spread thinly on the bark substratum. As it revives in a moist-chamber it quickly swells into a mucous-gelatinous layer, exactly like that of the first collection. This material offered a greater range of basidia, though mature ones were scarce. Very infrequently basidia of intercalary origin were found. The hypobasidia are often constricted. Figure 78 a-g outlines the structural plan for both collections.

Examination of the other herbarium specimens suggested emphasis of the following points. Usually the primordium of the basidium is of terminal origin, rarely it is intercalary. The hypobasidia are straight or constricted, but in a few collections irregular ones approaching the *H. pinicola* type occur. Micro-dimensions show a greater range than those given by Bourdot and Galzin, but they are fairly consistent for the particular collection. All the fructifications are decidedly gelatinous with a color range from Ochraceous-Buff to Fuscous, most commonly Grayish-Olive.

Bourdot and Galzin have included several varieties. Opportunity to examine a large number of collections of the species and the varieties *pruinosa* and *vulgaris* from Bourdot's herbarium showed that the varietal segregates are untenable on both habital and structural bases. According to Bourdot and Galzin, the variety *vulgaris* differs only in that it is "thinly spread in large gelatinous patches." When moistened it so appears; its color is pallid Cinnamon-Buff or Grayish-Olive. There is scarcely anything distinctive about this; certainly in structure it is identical with the parent species as shown by figure 77.

The variety *pruinosa* is segregated by these same authors on the bases of micro-dimensions and growth form. The measures of the hypobasidia in the material examined slightly exceed those cited by Bourdot and Galzin. Spore size extends from $8-11.5 \times 5-6.5 \mu$. Though the spore size of the parent species ranges from $8-18 \times 4-9 \mu$, the majority fall in a middle grouping around $9-11 \times 5-7 \mu$. It would be impossible to make a separation on spore size. The micro-dimensions do not distinguish the variety from the parent species; morphologically there is no difference between the two, and the color range is also closely parallel. No illustrations are included.

From the table following it is clear that there is more reason to set aside separate varieties than to maintain the former species because of differences in measurements. Such a criterion is hardly reliable in a group as variable as the heterobasidiomycetes.

HELICOGLOEA LAGERHEIMI PAT.

	Hyphae	Hypobasidium "sac"	Epibasidium	Spores
Type	2-6 μ	18-38 $\times$ 5.5-10 μ	69-100 $\times$ 5-7.5 μ	13-15-18 $\times$ 6.5-8 μ
Möller's measures	2-6 μ	30 $\times$ 8 μ	100 μ	13 $\times$ 7-9 μ
Rick's colls.	2-6 μ	18-33 $\times$ 6-7.5 μ	65 $\times$ 4.5 μ	15-18 $\times$ 6-7.5 μ
B.'s & G.'s measures	2-6 μ	18-30 $\times$ 6-9 μ	45-75 $\times$ 4-6.9 μ	8-10-15 $\times$ 5-6-8 μ
Other specimens	2-6 μ	15-39 $\times$ 5-13 μ	58-105 $\times$ 5-9 μ	8-12-17 $\times$ 4-9 μ
var. <i>vulgaris</i>	2-6 μ	18-28 $\times$ 5-8 μ	50-60 $\times$ 5-6 μ	9-11 $\times$ 6-7 μ
var. <i>pruinosa</i>	2-6 μ	16-32 $\times$ 5-9.5 μ	50-60 $\times$ 5-6 μ	8-11.5 $\times$ 5-6.5 μ
Roger's meas- ures	3-4.5-6 μ	16-32 $\times$ 7-10 μ	75-100 $\times$ 4.5-7.5 μ	11-14.5 $\times$ 5-7.5 μ
Total range	2-6 μ	15-39 $\times$ 5-13 μ	45-105 $\times$ 4-9 μ	8-18 $\times$ 4-9 μ

ECUADOR: Chorrera de Agoyan near Baños, Jan. 1892, *Lagerheim*, TYPE (in Farlow Herb. ex Herb. Patouillard).

BRAZIL: Rio Grande do Sul, São Leopoldo, 1931, *Rick* (in Farlow Herb.); 1931, *Rick* (in Herb. Mo. Bot. Gard.).

UNITED STATES: Iowa, Iowa City, Oct. 5, 1932, *Rogers*, 242; July 8, 1934, *Rogers*,

305, 306; July 9, 1934, *Rogers*, 274; Missouri, Springfield, Oct. 2, 1933, *Looney* (all in Herb. Univ. Iowa).

FRANCE: Allier, *Bourdot*, 5750 (in Farlow Herb. ex Herb. Patouillard); *Bourdot*, 5750, 5882, 39135 (in Herb. Paris ex Herb. Bourdot); Aveyron, *Galzin*, 3895, 3951, 4334, 5749, 7856, 7961, 10085, 11982, 13816, 13817, 14003, 14247, 14270, 14368, 14411, 14606, 14764, 14790, 14800, 14825, 14828, 16605, 16632, 16638, 16641, 16646, 16647, 16704, 16933, 17210, 17454, 18828, 18899, 19067, 20134, 21132, 23717, 23718, 23719 (in Herb. Paris, 23305, 6017, 6508, 7612, . . . , 23288, 23289, 23240, 12151, 12153, 12349, 12351, 12350, 23291, 23308, 23333, 23293, 12348, 12411, 23294, 23295, 23302, 23297, 23296, 23300, 23303, 23301, 23304, 23298, 23335, 14915, 15419, 15479, 15991, 18561, . . . , 24120, 24121, 24122); St. Gurol, May 6, 1910, *Galzin*, 5815 (in Herb. Paris, 23287 ex Herb. Bourdot); Tarn, July 23, 1909, *Galzin*, 4316 (in Herb. Paris, 23306 ex Herb. Bourdot); April 10, 1916, *Galzin*, 19561 (in Herb. Paris, 2331 ex Herb. Bourdot); St. Priest-en-Murat, Nov. 1914, *Bourdot*, 42262 (in Herb. Univ. N. Car. ex Herb. Bourdot); Orne, Oct. 1925, *E. Gilbert*, 1313 (in Herb. Paris, 39816 ex Herb. Bourdot).

ENGLAND: London, Feb. 1922, *Pearson* (in Herb. Paris ex Herb. Bourdot).

DISCUSSION

Mitotic processes of *Helicogloea* give no indications of abnormalities, although a few stages encountered need some exposition. The unusual spindle disposition in nuclear division is by no means restricted to this form. Kniep ('13) noted a similar irregularity in *Hypochnus terrestris*. His figures include a definitely crossed type and one slightly angled, both from a germ tube; and the usual conjugate type from the mycelium. This gradation is comparable to that found in the terminal hyphal cells of *Helicogloea*. Tischler (*l. c.*) adopted Kniep's figures; neither author offers an explanation. Neu-hoff ('24), throughout his studies on Auriculariaceae and Tremellaceae, saw mitosis only once—in *Achroomyces Tiliae*. Quite obviously, his illustration denotes that the spindles were crossed, but of this he makes no mention. However, he regards as abnormal crossed spindles in the hypobasidial division in *Exidia pithya*. This same phenomenon has been demonstrated frequently in the divisions of the fusion nucleus and in one instance of nuclear division in the spore (cf. *Rogers*, '32; *Lander*, '35; *Colson*, '35). That the clamp connection is a device to permit the side-by-side orientation of the spindles for the conjugate division of the dikaryon and a means to bring non-sister nuclei together, is widely accepted. Since there are

no clamp connections in this species, it is perhaps reasonable to assume that the crossing of the spindles is imposed by the narrow limits of the cell diameter.

Sass ('29) has commented upon the fact that apparently the chromatin masses at telophase become the nucleoli of the daughter nuclei. This is quite evidently so in the meiotic divisions of *Helicogloea* where a complete sequence can be traced easily from late anaphase to the reorganizing daughter nuclei, still joined by the drawn-out spindle threads. To explain this it is necessary to assume that the true nucleolus is distinct from this chromatic mass. This, then, would be in line with the second of the explanations offered by Sass for variation in chromosome and reticulum behavior among the several species that he was studying. In support of this hypothesis, that the chromatin is localized or stored in the large "nucleolus-like body" which therefore is to be considered a karyosome from which the chromatin passes into the achromatic framework during pre-meiotic processes, he presents four lines of evidence. Nuclei of *Helicogloea* are too small to permit confirmation. Sass's final statement, that the true nucleolus is a minute body expelled from the chromatin body just before spindle formation, offers a clue to what is evident in *Helicogloea*. As figures 45, 48 (cf. earlier stages also) show, there is a decided decrease in nucleolar size during prophasic periods evident from the first, and after the spindle and chromosomes are definitely formed a minute body is still visible, often some distance removed from the spindle. Later it too disappears. Though this cannot be conclusive without tracing the origin of the reticulum and chromosomes, nevertheless the behavior is suggestive. It seems to occur commonly in many fungi; Wakayama ('30) has promoted similar ideas based on observations of *Aspergillus*.

One of the most curious and striking of aberrations concerns the chromosomes in their passage to the poles. This consistently is irregular, so that from metaphase through anaphase they are scattered from equator to pole, sometimes more or less clumped together. Throughout the literature

this condition is commonly figured (cf. Juel, '98; Ruhland, '01; Kniep, '13; Colley, '18; Bagchee, '25; Wakayama, '30, '30a, '31, '32) not only for basidiomycetes but for ascomycetes as well. Wakayama's extensive works, especially on Agaricaceae, show that this phenomenon is more characteristically present than a regular separation of the chromosomes. His comment that this scattering is due to very different migration velocities for each univalent is the only stated attempt noted in elucidation of the point. He furthermore remarks that in spite of this unusual procedure it nowise follows that the nuclear process is not typical.

Even more striking than this is the behavior of the nuclei in their migration from the parent cells or accessory appendages into the spores. Their extreme chromaticity, attenuation, and loss of form mark the narrow constricted portion through which they must pass just prior to entering the spore as a true sterigma, *sensu* Neuhoff. Such nuclear alteration has been remarked time and time again in the basidiomycetes. Maire ('02) noted that in the heterobasidiomycetes the nucleus passed into the germ tube without change but in moving into the spore through the sterigma it became constricted. It remained for Neuhoff, however, to crystallize the phenomenon into a definite criterion. According to his dictum, cytological in its foundation, a migrating nucleus in passing through a sterigma into a spore assumes just such an elongated form, at the same time giving a chromatin stain reaction. It is tenable then that the long inflated appendages so frequently developed in place of the shorter subulate sterigmata are accessory. This is strengthened still more by the fact that when they reach the surface or a position favorable to spore discharge true sterigmata are formed and the nuclei go through them into the spores in the changed form. That such attenuation is not the result of mechanical constriction due to the size of the sterigma is upheld by the initiation of the condition long before the nucleus reaches that portion of the sterigma (cf. Whelden, '34, on *Tremella*). Spore germination processes are initiated by the production from the primary spore of filaments of varying

length. This in turn develops a true sterigma through which the nucleus moves into the secondary spore, having previously undergone precisely these specified changes. The sterigmata in relation to the spores by all evidence fit Buller's ('22) functional criteria, viz., that "the typical sterigma . . . is . . . an organ for the violent discharge of the spores." The hilum region of the *Helicogloea* spore is well developed. Observation of the actual mechanism of discharge was impossible without fresh material.

A lack of consistency in the terminology employed for the basidiomycetes and the interpretation of their diagnostic structure, the basidium, has long marked the literature, the situation only recently becoming clarified and more constant as careful morphological and cytological studies have brought out true and natural relationships. *Helicogloea* is classified with those basidiomycetes which have transversely septate basidia as opposed to those in which the basidia are vertically divided or those which remain undivided. Historically, the basidiomycetes have been separated into various subdivisions on the basis of basidium morphology, e. g., Hyménomycètes-Hétérobasidiés and Homobasidiés (Patouillard, '87); Proto- and Autobasidiomycetes (Brefeld, '88); and Acrosporeae and Pleurosporeae (van Tieghem, '93). As Gäumann and Dodge (*l. c.*) point out, the first two complements carry a phylogenetic implication and the last is neutral in its connotation. These categories do not comprise identical groups. Van Tieghem considered septum formation an accessory character, the fundamental one for him being the mode of spore insertion, expressed by his terms Acrosporeae and Pleurosporeae. These primary divisions each included both septate and non-septate basidia, which he spoke of as Phragmo- and Holobasidia. Patouillard's groupings have a less artificial basis. Furthermore, he recognized in distinguishing between hetero- and homobasidial groups that the spores of the former usually germinate by the production of secondary spores, whereas those of the latter germinate by mycelia. Such a distinction is a more reliable criterion for primary segregation of the ba-

sidiomycetes than the character of septation. In recent years the use of the terms heterobasidiomycetes and homobasidiomycetes has found acceptance. The heterobasidiomycetes include those forms with secondary spore germination and basidia usually divided in some fashion—the notable exception being the undivided basidia found in the Dacrymycetaceae.

At its earliest inception the basidium of *Helicogloea*, or that of almost any heterobasidiomycete, is not distinguishable from one of a homobasidiomycete at a comparable level of development. Both are usually single, terminal hyphal cells containing a pair of nuclei, descendants of the dikaryon of the sub-terminal cell. From this point onwards the resemblance is diminished in a greater or lesser degree. The true homobasidium remains undivided and develops no accessory parts. Therefore it functions both as zeugite and gonotocont. Variation in some of the heterobasidiomycetes is founded on the separation of these critical stages and consequent modification of morphological patterns.

In *Helicogloea* the initial cell of the basidium complex has been designated as the primordium, a term not inappropriate for the same stage of the homobasidium. From here on the similarity ceases. The subsequent development in the heterobasidiomycetes, and in particular in the genus under discussion, involves the production of distinct and often persistent morphological entities. For *Helicogloea* these take the form of the “sac” and of spore-producing out-growths. Möller called the former “tragzelle,” thus merely indicating its position and form with no intimation of its cytological significance. Van Tieghem’s terms—probasidium and basidium—have been more widely adopted by later workers. Their connotation does not permit the probasidium as part of the basidium proper and hence introduces a misleading idea of their true relation to the nuclear functions. For this reason they are rejected here. Probasidium, promycelium, and basidium have also been applied to the different parts of the basidium, especially by those who were particularly impressed by the striking resemblances of the group to certain Uredinales.

These terms are rejected on the same basis as the preceding ones.

A cytological interpretation is credited to Wettstein ('11), who emphasized the fact that in the basidium the fusion of two nuclei takes place before the formation of the spores. As Rogers ('34) has stated, the most satisfactory concept of the basidium—for both homo- and hetero-types—is Neuhoff's (*l. c.*). It is basically cytologic, for he considers the morphological development consequent upon that. According to that author, the mature basidium of the heterobasidiomycetes is composed of a *hypobasidium* which has "germinated" to one or more appendages, the *epibasidia*. This terminology allows adequately for any morphological separation of karyogamy and meiosis. If both these critical events take place in the hypobasidium several epibasidia result, usually four, sometimes eight, consequent upon the number of nuclei produced—as in the Tremellaceae and Tulasnellaceae, respectively; if meiosis is delayed until after germination there is produced, naturally, only one epibasidium. In the latter category are placed the Auriculariaceae, and, among them, *Helicogloea*.

It is a simple matter to reconcile the situation in that genus with this conception. Neuhoff defines the hypobasidium as the "lower, commonly inflated vesicular part of the basidium"; the epibasidium as the "upper, more uniformly tubular part of the basidium." The two parts are in the majority of instances in free communication at all times. If this ground-plan is applied to the behavior in *Helicogloea* all the species resolve neatly into that scheme. That is, the "sac," a lateral expansion of the primordium, is the place where the two nuclei come together and fuse, and therefore it is truly hypobasidial. From the primordium is produced apically a single appendage in which the secondary nucleus undergoes meiosis, the whole eventually elongating and bearing sterigmata and spores. This quite properly is the epibasidium. The two parts are never separated but are at all times in open communication. Even for those species in which the primordium is intercalary this holds. It is evident then that there is nothing in Neuhoff's

criteria to exclude their general application to *Helicogloea*. At first there may seem to be a morphological discrepancy which would prevent their literal adoption. Apparently only those forms with direct germination of the primordium without an accessory part—and the clavate hypobasidium of *H. intermedia* is the only one which answers that description—seem to be completely in harmony with Neuhoﬀ's principles. However, it is only necessary to include for the others the primordial portion as part of the hypobasidium, which therefore is to be described as a hypobasidium with a lateral expansion. In the light of this interpretation the production of the epibasidium is seen to be from the hypobasidium, whatever the constitution of the latter (cf. *H. pinicola*, *H. intermedia*, and *H. Lagerheimi*).

There is good morphological justification for this. The primordium and sac are plainly complementary parts of one structure, and the epibasidium, an outgrowth from either part, is filled with protoplasm at their expense. For reasons of convenience the term primordium is retained to cover the primary phase of the hypobasidium; likewise, the accessory development where karyogamy occurs is referred to as the hypobasidium and in formation is secondary. This is the only example so far known in which there is such an obvious morphological separation of the initial portion of the hypobasidium from that in which karyogamy occurs. One minor deviation from Neuhoﬀ's nuclear scheme must be noted. The secondary nuclei of those Auriculariaceae which he investigated characteristically began migration into the epibasidium during the post-synaptic stage of the first meiotic division. In *Helicogloea* the fusion nucleus contracts to a typical resting condition and then migrates into the epibasidium where it undergoes meiosis. In other words, not only is the hypobasidium divided into two distinct units, a condition not known in other Auriculariaceae, but the nuclear cycle is interrupted by a resting stage—even though it is so short it clearly is only to allow for migration.

The hypobasidium of *Helicogloea* has often been interpreted as a storage organ, an ecological view which Möller inaugu-

rated. His statement that the contents of the hypobasidium would be withdrawn completely and migrate into the developing epibasidium was based on accurate observation, it is true. The idea of a storage organ, unique for this genus, was again expressed by Gäumann ('22). But obviously the time relation between fusion and migration of the secondary nucleus (it contracts and rests only long enough to orient itself for emigration) precludes such an interpretation. One must admit, though, that by virtue of this behavior there is introduced the potentiality for a longer resting period. That the hypobasidium is not a storage organ, in which reserves are held in readiness to produce the epibasidium when favorable conditions so permit, is further substantiated by the observation that as often as not epibasidial germination and elongation occur without any visible augmentation from the hypobasidium. The complementary parts of the hypobasidium are to be construed, then, only in the light of the nuclear cycle.

Within the genus itself there is manifested in basidial characters a progressive sequence from simpler to more advanced forms. Quite obviously, the least developed type would be the clavate form of *Helicogloea intermedia*. The basidium arises as a terminal primordium, becomes swollen to accommodate karyogamy, and then germinates directly to the epibasidium. Here, then, is the simplest type of hypobasidium found in the group, for it consists of only one morphological entity. It is significant that, according to Linder's notations, this type of hypobasidium is the first produced. Since there is a saccate type of hypobasidium in the same species, the production of the clavate type takes on a vestigial aspect. Rogers ('34), going on the assumption that the "primitive auriculariaceous basidium is one with a persistent hypobasidium, clearly distinguishable in all stages," uses as an example the saccate *Helicogloea* hypobasidium showing distal germination. Such behavior is decidedly atypical if it occurs at all. The clavate form is much more acceptable as the primitive type of auriculariaceous basidium, for its hypobasidium is a sharply delimited, persistent organ. Second, there may be placed the

type characteristic of the majority of species, *H. Lagerheimi*, *H. graminicola*, and *H. caroliniana*, whose basidial primordia likewise are terminal, but which give rise to a secondary part, morphologically distinct. Advance is also indicated by the fact that the clavate type shows no adjustment for proliferation, whereas in the second type there is ample allowance through the subterminal cell development. The remaining species are all marked by this division of the hypobasidium into primary and secondary portions. *H. pinicola* shows an entirely new departure in the intercalary origin of the basidium. But nevertheless the primary portion of the hypobasidium remains the source of germination. (Note that infrequently this pattern is found in the preceding species, too). In the saccate type of *H. intermedia* it is the secondary portion of the hypobasidium which germinates. This possibly represents the highest level, for it suggests a potentiality for a resting stage, and, through encystment, eventual separation. In all types meiosis occurs in the epibasidium.

It is evident that the hypobasidium, and in particular the secondary portion thereof, is the critical organ of the genus. Cytologically this has been shown to be the place of karyogamy followed by contraction to the resting condition. Phylogenetically it offers two lines of interpretation: either reduced or increasing development. Both ideas are extant in the literature as applied to relationships within the Auriculariaceae, and between them and other groups.

In the Auriculariaceae, Neuhoﬀ constructs a phylogenetic scheme involving both tendencies. He considers the genus *Iola* the crucial one, for there the basidium arises from a terminal cell and is divided into hypobasidium and epibasidium, the former remaining distinct. This gives rise to two main lines, one showing reduction in differentiation of the hypobasidium, the other increasing emphasis. The first of these is subdivided into a series in which reduction eventually leads to complete suppression, as illustrated by the genus *Helicobasidium*; and another in which the hypobasidium is present though it may be reduced to a vestigial condition, as read in the series

Achroomyces, *Tjibodasia*, and *Auricularia*. The second line emphasizes the hypobasidium through the thickening of its walls and the introduction thereby of a resting period. This plan of development is illustrated by the genera *Cystobasidium* and *Septobasidium*. In the latter there are especially critical characters, for the thickening of the walls in some species is so advanced that in view of that and a consequent resting period, the hypobasidium is known as a sclerobasidium. This condition then is strongly like that of the rust teliospore. Indeed, the only real basidial difference between this and such primitive rusts as *Gallowaya* is the catenulate nature of the teliospores of the latter. Consequently, Neuhoﬀ sees here a direct link to the Uredinales through such a genus, for instance, as *Uromyces*, whose teliospores are borne singly on the hyphae. Hence the sclerobasidium (encysted hypobasidium) and the teliospore are homologous.

That there is a close relationship between the Auriculariaceae and the Uredinales is argued by more than mere analogy. Cytologically it is demonstrable that the teliospore and hypobasidium are strictly homologous; likewise the promycelium and epibasidium; sporidia and basidiospores. Möller was the first to comment on this, but to him the hypobasidium of *Helicogloea* and the teliospore were homologous because both were the assembling point of materials necessary for basidium production. Since in the former no resting period was involved there was no need for a heavy wall. This ecological interpretation has since been replaced by the more substantial cytological one. Moreover, the ecological argument lost credibility as investigations revealed that the teliospore is not necessarily designed for wintering over, for there are rusts whose teliospores germinate at once. Again there are rusts whose teliospores are thin-walled, just as in *Septobasidium* of the Auriculariaceae, where the development passes from species with thin-walled, non-resting hypobasidia—hardly more than a stage in development—to thick-walled, persistent forms which rest (winter-over) before germinating. Such striking parallelisms emphasize the closeness of the auriculariaceous fungi and the rusts.

The majority of writers have adhered to de Bary's ('84) tenets that the Uredinales constitute the most primitive of the basidiomycetes. Recently Linder ('29) and Pady ('33) have stressed this by deriving the auriculariaceous forms from the Uredinales. Thus Linder, starting with the Uredinales would, by reduction of the hypobasidium, lead the developmental line through *Septobasidium* and *Cystobasidium* to *Iola* with secondary branches to *Helicogloea* and *Auricularia*. *Septobasidium* holds the closest connection with rusts, since it is parasitic. It stands as a source of further development by reason of two different hypobasidial expressions: thick-walled forms which are adapted for wintering-over and thin-walled forms which have no resting period prior to germination and which really are no more than a stage in development. The latter affords a link to *Iola*, a parasitic form whose thin-walled hypobasidia likewise germinate at once. *Helicogloea* has lost both the parasitic habit and the thickened hypobasidia. *Auricularia* is even more reduced, for there the hypobasidium is represented only as a stage. Specifically, by virtue of the clavate type of hypobasidium, Linder regarded *Helicogloea intermedia* as the form transitional between the rusts and *Iola*. To achieve such a step from rusts to auriculariaceous species, there must be postulated the concomitant factors—reduction of aeciospores to binucleate conidia, development of an extensive fruiting body, and finally a change from parasitic to saprobic habit.

In opposition to such a derivative scheme it may be contended that it is more logical to derive aeciospores from binucleate conidia. This Neuhoff has expressed when he homologized the aeciospores with diploid conidia known in the Auriculariaceae and the pycniospores with haploid conidia. Thus the variety of secondary spore forms in the rusts cannot be said to constitute an obstacle to relationships between the two groups in light of the occurrence of both haploid and diploid conidia in the Tremellales. Especially does the argument of transition from parasitic to saprobic habit seem untenable. As Janchen ('23) has remarked, an attempt at

phylogenetic elucidation must be not only morphologically acceptable, but ecologically comprehensible as well, if it is to be satisfactory. And exactly in its ecological expression does this derivation of Auriculariaceae from Uredinales seem to fail. The high specialization attained by the rusts much more clearly marks them as an end term of a series than as a derivation point. The reverse derivation—the rusts from auriculariaceae forms—is not inconceivable ecologically when one considers the numerous examples of parasitic species of Auriculariaceae.

The foregoing discussion is intended only to summarize some of the more outstanding phylogenetic interpretations in the literature. In view of the greater defensibility of the derivation of the rusts from the Auriculariaceae, that plan is upheld. *Helicogloea* is regarded therefore as representing a simple auriculariaceae type showing tendencies which could lead to the development of an independent hypobasidium and hence to a true teliospore.

SUMMARY

1. *Helicogloea* Pat. takes precedence over *Saccoblastia* Möll. with corresponding transfer of recognized species. *Saccoblastia ovispora* and *S. sebacea* are both regarded as synonyms of *Helicogloea Lagerheimi* Pat.

2. In *Helicogloea Lagerheimi* Pat. the basidial primordium is a two-nucleate hyphal cell, producing a lateral expansion.

3. The dikaryon migrates into the expanded portion of the hypobasidium where fusion takes place.

4. Following contraction to the resting condition the secondary nucleus migrates through the primordial portion into the elongating epibasidium, which has arisen apically from the primordium.

5. The two meiotic divisions always take place in the enlarged portion of the epibasidium. The latter segments into four cells and each segment produces a sterigma and a spore or an accessory appendage bearing a sterigma and a spore.

6. Spore germination is by repetition.

7. Morphological development is various in relation to the nuclear cycle; it has been found to correspond to one of three patterns, designated as I, II, and III.

8. The basidium complex is composed of hypobasidium and epibasidium, *sensu* Neuhoﬀ. The former comprises two morphologically distinct parts: the primordium, or primary portion, and its lateral expansion, the "sac," or secondary portion.

9. Within the genus there is seen a progressive sequence from simpler to more advanced forms of basidia, the clavate hypobasidium of *H. intermedia* being interpreted as the most primitive.

This study was done at the Henry Shaw School of Botany of Washington University. The writer takes pleasure in acknowledging the facilities thereby extended, and the assistance of Dr. C. W. Dodge, under whose direction the work was done. Especial acknowledgments are due Dr. Donald P. Rogers, formerly of the Department of Botany, State University of Iowa, not only for the collections and their preparation which made possible the investigation, but for locating the type of *Helicogloea Lagerheimi* Pat. Thanks are also extended to those institutions which so generously lent of their herbarium materials.

LITERATURE CITED

- Bagchee, K. ('25). Cytology of the Ascomycetes. *Pustularia balarioides* Ramsb. Ann. Bot. **39**: 217-266. 1925.
- Bary, A. de. ('84). Vergleichende Morphologie und Biologie der Pilze, Mycetozen, und Bacterien. Leipzig, 1884.
- Bensaude, M. ('18). Recherches sur le cycle evolutif et la sexualité chez les Basidiomycètes. Thèse. Paris, 1918.
- Blackman, V. H. ('04). On the fertilization, alternation of generations, and general cytology of the Uredineae. Ann. Bot. **18**: 323-373. 1904.
- Bourdot, H. ('32). Hyménomycètes nouveaux ou peu connus. Soc. Myc. Fr. Bull. **48**: 204-232. 1932.
- , et A. Galzin. ('09). Hyménomycètes de France. I. Hétérobasidiés. *Ibid.* **25**: 15-36. 1909.
- , ———, ('28). Hyménomycètes de France. Sceaux, 1928.
- Brefeld, O. ('88). Untersuchungen aus dem Gesamtgebiete der Mykologie. VII. Leipzig, 1888.
- Bresadola, J. ('03). Fungi polonici. Ann. Myc. **1**: 97-131. 1903.

- Buller, A. H. R. ('22). Researches on fungi. 2. London, 1922.
- Chamberlain, C. J. ('32). Methods in plant histology. ed. 5. Chicago, 1932.
- Clements, F. E. ('09). The genera of fungi. Minneapolis, 1909.
- , and C. L. Shear. ('31). The genera of fungi. New York, 1931.
- Coker, W. C. ('20). Notes on the lower Basidiomycetes of North Carolina. Jour. Elisha Mitchell Sci. Soc. 35: 113-182. 1920.
- Colley, R. H. ('18). Parasitism, morphology, and cytology of *Cronartium ribicola*. Jour. Agr. Res. 15: 619-659. 1918.
- Colson, B. ('35). The cytology of the mushroom *Psalliota campestris* Quel. Ann. Bot. 49: 1-18. 1935.
- , ('28). Notes on Basidiomycetes. Ibid. 43: 233-248. 1928.
- Ferry, R. ('96). Les Protobasidiomycètes du Brésil. Rev. Myc. 18: 101-113. 1896.
- Gäumann, E. ('22). Über die Entwicklungsgeschichte von *Jola javensis* Pat. Ann. Myc. 20: 272-289. 1922.
- , and C. W. Dodge. ('28). Comparative morphology of fungi. New York, 1928.
- Janchen, E. ('23). Die Stellung der Uredineen und Ustilagineen im System der Pilze. Österr. Bot. Zeitschr. 72: 302-304. 1923.
- Juel, H. O. ('98). Die Kerntheilungen in den Basidien und die Phylogenie der Basidiomyceten. Jahrb. f. Wiss. Bot. 32: 361-388. 1898.
- Killermann, S. ('28). Eubasidii. In Engler u. Prantl. Die Natur. Pflanzenfam. 2 Aufl. 6: 99-283. 1928.
- Kniep, H. ('13). Beiträge zur Kenntnis der Hymenomyceten I & II. Zeitschr. f. Bot. 5: 593-637. 1913.
- Lander, C. A. ('35). The development of the fruiting body of *Arachnion album*. Jour. Elisha Mitchell Sci. Soc. 50: 275-282. 1935.
- Lindau, G. ('97). Phacidiineae. In Engler u. Prantl. Die Natur. Pflanzenfam. I. 1: 243-265. 1897.
- Linder, D. H. ('29). Life-history and cytology of *Saccoblastia intermedia* n. sp. Ann. Mo. Bot. Gard. 16: 487-494. 1929.
- Lindfors, T. ('24). Studien über den Entwicklungsverlauf bei einigen Rostpilzen aus zytologischen und anatomischen Gesichtspunkten. Svensk. Bot. Tidskr. 18: 1-84. 1924.
- Maire, R. ('02). Recherches cytologiques et taxonomiques sur les Basidiomycètes. Soc. Myc. Fr. Bull. Suppl. 18: 1-210. 1902.
- Martin, G. W. ('34). The genus *Stypella*. Univ. Iowa Studies Nat. Hist. 16: 143-149. 1934.
- Möller, Alfred. ('95). Protobasidiomyceten. Bot. Mitt. a. d. Tropen 8: 1-179. 1895.
- Neuhoff, W. ('24). Zytologie und systematische Stellung der Auriculariaceen und Tremellaceen. Bot. Archiv 8: 250-297. 1924.
- Pady, S. M. ('33). Teliospore development in the Pucciniastreae. Can. Jour. Res. 9: 458-485. 1933.
- , ('34). Meiosis in *Milesia marginalis*. Bull. Torrey Bot. Club. 61: 345-354. 1934.
- , ('35). A cytological study of the development and germination of the teliospores of *Hyalopsora aspidiotus* (Pk.) Magn. Ann. Bot. 49: 71-93. 1935.

- Patouillard, N. ('87). Les Hyménomycètes d'Europe. Paris, 1887.
- , et G. de Lagerheim. ('92). Champignons de l'équateur. Soc. Myc. Fr. Bull. **8**: 113-140. 1892.
- , ('00). Essai taxonomique sur les familles et les genres des Hyménomycètes. Lons-le-Saunier, 1900.
- Rick, J. ('33). Monografia dos protobasidiomicetos Rio-Grandenses. *Egatea* **18**: 209-215, 285-288, 343-349. 1933.
- Rogers, D. P. ('32). A cytological study of *Tulasnella*. Bot. Gaz. **94**: 66-105. 1932.
- ('33). Some noteworthy fungi from Iowa. Univ. Iowa Studies Nat. Hist. **15**: 9-29. 1933.
- , ('34). The basidium. *Ibid.* **16**: 160-181. 1934.
- Ruhland, N. ('01). Zur Kenntnis der intracellularen Karyogamie bei den Basidiomyceten. Bot. Zeit. **59**: 187-206. 1901.
- Saccardo, P. A. ('82). Sylloge fungorum. **14**: 245. Padua, 1882.
- Sass, J. E. ('29). The cytological basis for homothallism and heterothallism in the Agaricaceae. Am. Jour. Bot. **16**: 663-701. 1929.
- Sharp, L. W. ('34). Introduction to cytology. ed. 3. New York, 1934.
- Tieghem, P. van. ('93). Sur la classification des Basidiomycètes. Jour. de Bot. **7**: 77-87. 1893.
- Tischler, G. ('21-'22). Handbuch der Pflanzenanatomie. **2**: Allgemeine Pflanzenkaryologie. 1921-1922.
- Wakayama, K. ('30). Contributions to the cytology of fungi. I. Chromosome number in Agaricaceae. *Cytologia* **1**: 369-388. 1930.
- , ('30a). *Ibid.* II. Cytological studies in *Morchella deliciosa* Fr. *Ibid.* **2**: 27-36. 1930.
- , ('31). *Ibid.* III. Chromosome number in *Aspergillus*. *Ibid.* **2**: 291-302. 1931.
- , ('32). *Ibid.* IV. Chromosome number in Autobasidiomycetes. *Ibid.* **3**: 260-284. 1932.
- Wakefield, E., and A. A. Pearson. ('23). Some additional records of Surrey resupinate Hymenomycetes. Brit. Myc. Soc. Trans. **8**: 216-221. 1923.
- Wettstein, F. ('11). Handbuch der systematischen Botanik. ed. 2. 1911.
- Whelden, R. M., ('34). Cytological studies in the Tremellaceae. I. *Tremella*. *Mycologia* **26**: 415-435. 1934.

EXPLANATION OF PLATE

PLATE 7

Helicogloea Lagerheimi

All figures have been drawn with the aid of an Abbé camera lucida. Magnifications are given for each figure.

Figs. 1-13 inclusive show the morphological development of the basidium from the primordial stage through the mature basidium with spores. The nuclear conditions are representative only for these particular examples. All figures $\times 1100$.

Fig. 1. Enlarged terminal hyphal cell, the basidial primordium, with two nuclei.

Fig. 2. Production of the hypobasidium as a lateral expansion of the primordium.

Fig. 3. Hypobasidium enlarging, the nuclei moving toward the enlarging secondary portion of the hypobasidium.

Fig. 4. Mature hypobasidium with two nuclei in it.

Fig. 5. Mature hypobasidium with fusion nucleus; epibasidium arising at the apical end of the primordium.

Fig. 6. Nucleus migrating through the primordium; hypobasidium collapsing as the protoplasm withdraws; epibasidium elongating.

Fig. 7. Continued elongation of the epibasidium and withdrawal of protoplasm from the hypobasidium.

Fig. 8. Nucleus in enlarging epibasidium; hypobasidium entirely empty.

Fig. 9. Enlarging epibasidium.

Fig. 10. Epibasidium bending over.

Fig. 11. Epibasidium two-septate, following the first meiotic division; protoplasm withdrawn partly from lower portions.

Fig. 12. Epibasidium three-septate, 4-nucleate; budding sterigmata; the lower portions of the epibasidium collapsing, completely drained of protoplasm.

Fig. 13. Mature basidium with spores in place.

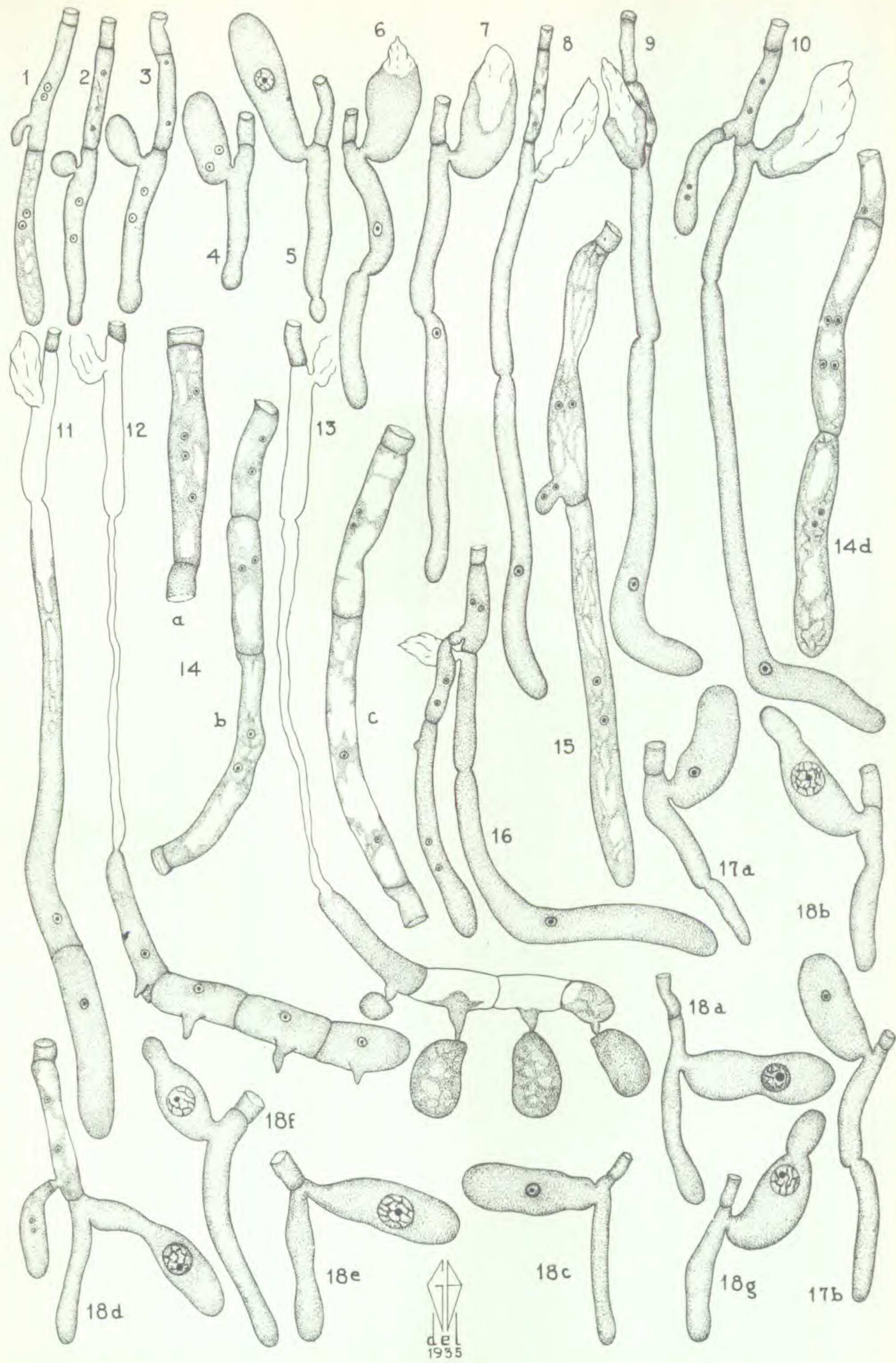
Fig. 14. Hyphal cells. a, d, young cells in which four nuclei are present, for the wall is not yet formed; b, c, older cells with increased reduction of protoplasm. $\times 1865$.

Fig. 15. Origin of a branch from a subterminal cell; the terminal cell constitutes a basidial primordium. $\times 1865$.

Fig. 16. Basidial proliferation. (See also fig. 18d.) $\times 1100$.

Fig. 17. Developing epibasidia showing a crimp between the epibasidium and hypobasidium. $\times 1100$.

Fig. 18. Variations in hypobasidial form. a, b, constricted hypobasidia; c, horizontal hypobasidium; d, e, pendent hypobasidia; f, g, extreme distal constriction. $\times 1100$.



BAKER — HELICOGLOEA

EXPLANATION OF PLATE

PLATE 8

Helicogloea Lagerheimi

Fig. 19. Composite view of the fructification on a wood substratum as seen in section. $\times 464$.

Fig. 20. Scales to illustrate the proportion of fruiting and hyphal regions in differently developed fructifications. $\times 100$.

Fig. 21. a, b, basidia arising from lateral branches. $\times 1100$.

Fig. 22. Origin of epibasidium prior to appearance of hypobasidium. $\times 1865$.

Fig. 23. a, b, c, irregular, lateral production of epibasidia. Surface level of the fructification marked. $\times 1100$.

Fig. 24. Type I of nuclear migration from the hypobasidium. $\times 1100$.

Fig. 25. Type II of nuclear migration from the hypobasidium. a, typical form; b, unconstricted type.

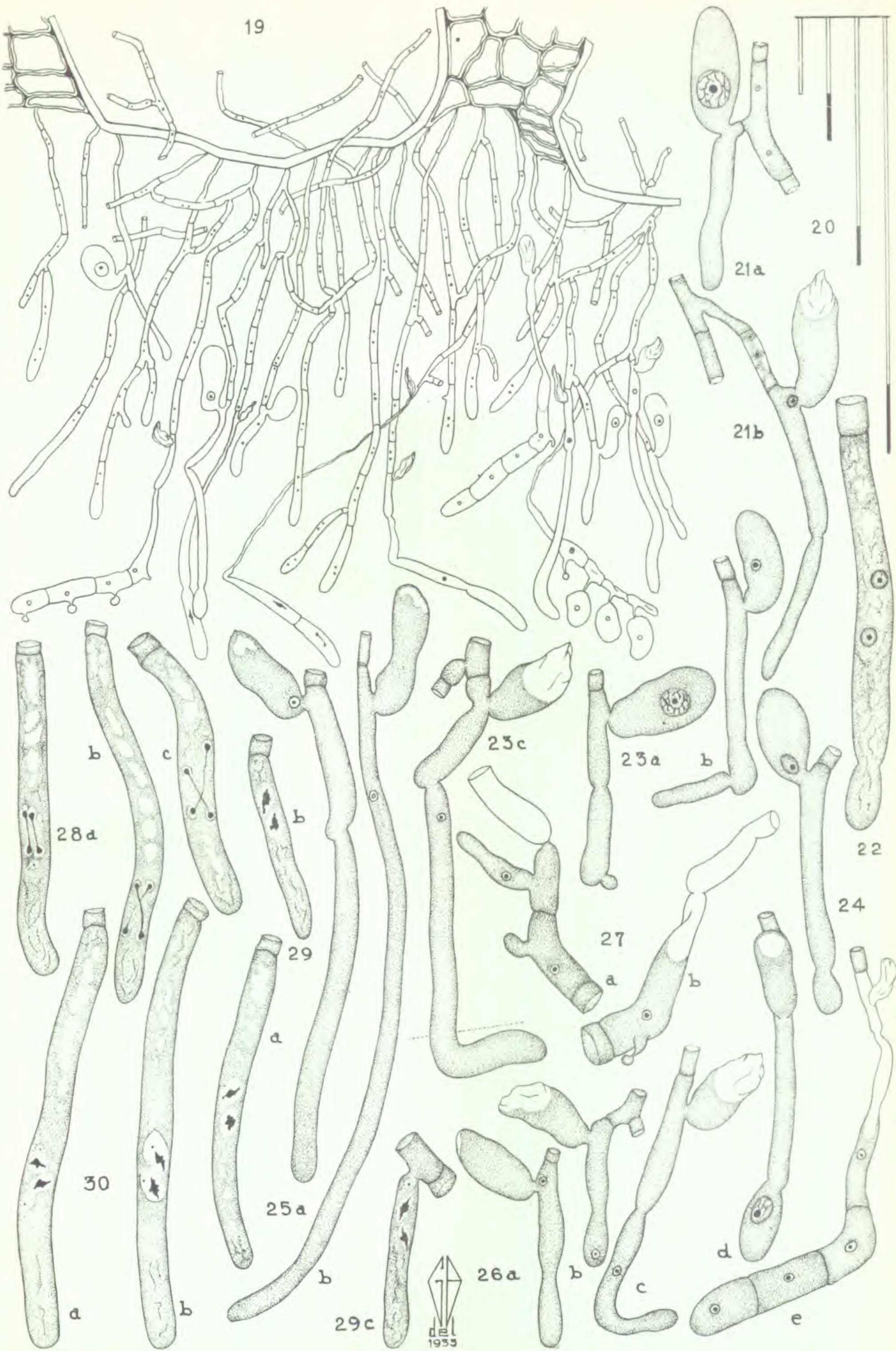
Fig. 26. a, Type III of nuclear migration. b, c, d, e, subsequent development.

Fig. 27. a, deep constriction and septum at the base of the fourth segment of the epibasidium; b, constriction without a wall. $\times 1100$.

Fig. 28. a, conjugate mitosis, with nearly parallel orientation; b, c, crossed spindles. $\times 1865$.

Fig. 29. a, b, c, mitotic division figures indicating future crossed orientation of the spindles. In c a remnant of the nucleolus is visible. $\times 1865$.

Fig. 30. Mitosis. a, membranes completely broken down, nucleoli still visible; b, nuclear membranes present in part, nucleoli distinct. $\times 1865$.



BAKER — HELICOGLOEA

EXPLANATION OF PLATE

PLATE 9

Helicogloea Lagerheimi

Fig. 31. a, basidial primordium with the basal wall just formed; b, older primordium with hypobasidium and epibasidium both developing. $\times 1865$.

Fig. 32. A series to show the increase in size from the initiation of the primordium through the hypobasidium production. $\times 1865$.

Fig. 33. Origin of the hypobasidium. (See also fig. 31b.) $\times 1865$.

Fig. 34. a, b, nuclei in close association previous to migration into the hypobasidium. $\times 1865$.

Fig. 35. Lag of second nucleus in passage into hypobasidium. $\times 1865$.

Fig. 36. a, b, nuclei moving into hypobasidium. In b the first nucleus is prematurely enlarged prior to fusion. $\times 1865$.

Fig. 37. Nuclei in hypobasidium previous to fusion. Note effect of streaming protoplasm. $\times 1865$.

Fig. 38. Nuclear fusion. a, nuclei touching, nuclear membranes still intact; b, nuclei as in a, but enlarged and showing a reticulate nature; c, nuclear membranes broken down and the contents mingling; d, nuclei fusing, one larger than the other with slightly more pronounced reticulations; e, nuclei of different sizes corresponding to their development, both deeper in the hypobasidium than usual. $\times 1865$.

Fig. 39. Fused nuclei with an indentation between the two still apparent. Within the common membrane there is an advancing net development. $\times 1865$.

Fig. 40. a, b, c, stages in nucleolar fusion. $\times 1865$.

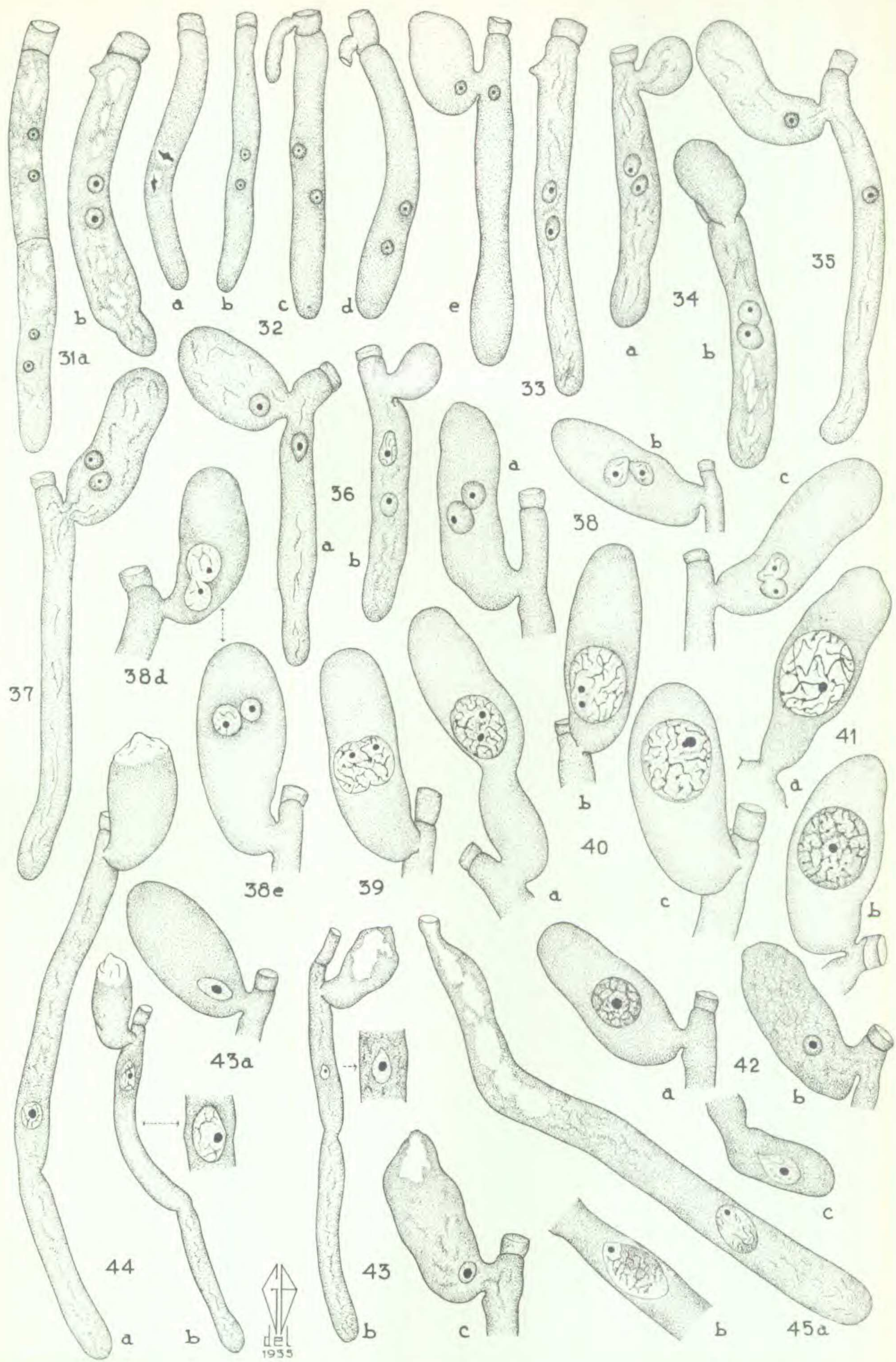
Fig. 41. a, post-fusion nucleus, with strongly developed network; b, post-fusion nucleus with prominent chromatic beads scattered on the threads. $\times 1865$.

Fig. 42. a, nucleus contracting, the network still pronounced; b, nucleus in resting condition, completely contracted. $\times 1865$.

Fig. 43. a, b, c, examples of nuclear passage from hypobasidium; a, detail of fig. 24; c, detail of fig. 25. $\times 1865$.

Fig. 44. Variation in the initiation of prophase activity. a, nucleus enlarged, reticulate. $\times 1865$. b, nucleus still in primordial portion. $\times 1100$ with detail $\times 1865$.

Fig. 45. Prophase in sporogenous part of the epibasidium. a, nuclear membrane intact, nucleolus peripheral, network appearing opposite pole of nucleolus; b, the network appearing slightly polarized; c, faint reticulations in enlarged nucleus from epibasidium of Type III. All $\times 1865$.



BAKER — HELICOGLOEA

EXPLANATION OF PLATE

PLATE 10

Helicogloea Lagerheimi

Fig. 46. Prophase of first meiotic division. The nucleus is elongate, conforming to the shape of the epibasidium. $\times 1100$ with detail $\times 1865$.

Fig. 47. Early prophase with chromatic beads on the threads. $\times 1865$.

Fig. 48. Prophase. a, nucleolus, slightly diminished in size, lying at anterior pole and the threads grouped at the opposite pole. $\times 1865$; b, nucleolus still prominent, the threads less massed and central in position. $\times 1100$ with detail $\times 1865$; c, later prophase, the nucleolus at the periphery, the chromatin densely massed. $\times 1865$.

Fig. 49. Early prophase from an epibasidium with a development corresponding to Type III. $\times 1865$.

Fig. 50. Anaphase. a, intranuclear spindle with scattered chromosomes. Remnants of the nucleolus are visible within the membrane and centrosomes are present at the poles. b, nuclear membrane present in part; nucleolus sharp; c, d, e, membranes broken down and spindles free in cytoplasm; the nuclei have disappeared. $\times 1865$.

Fig. 51. Late anaphase. a, nuclear membrane discernible in part, the nucleolus distinct in the cytoplasm; b, membrane entirely gone, chromosomes massing together as they move to the poles; c, spindle contracted, chromosomes clumped, massing at the poles. The clearer areas at the poles denote the position of the daughter nuclei. $\times 1865$.

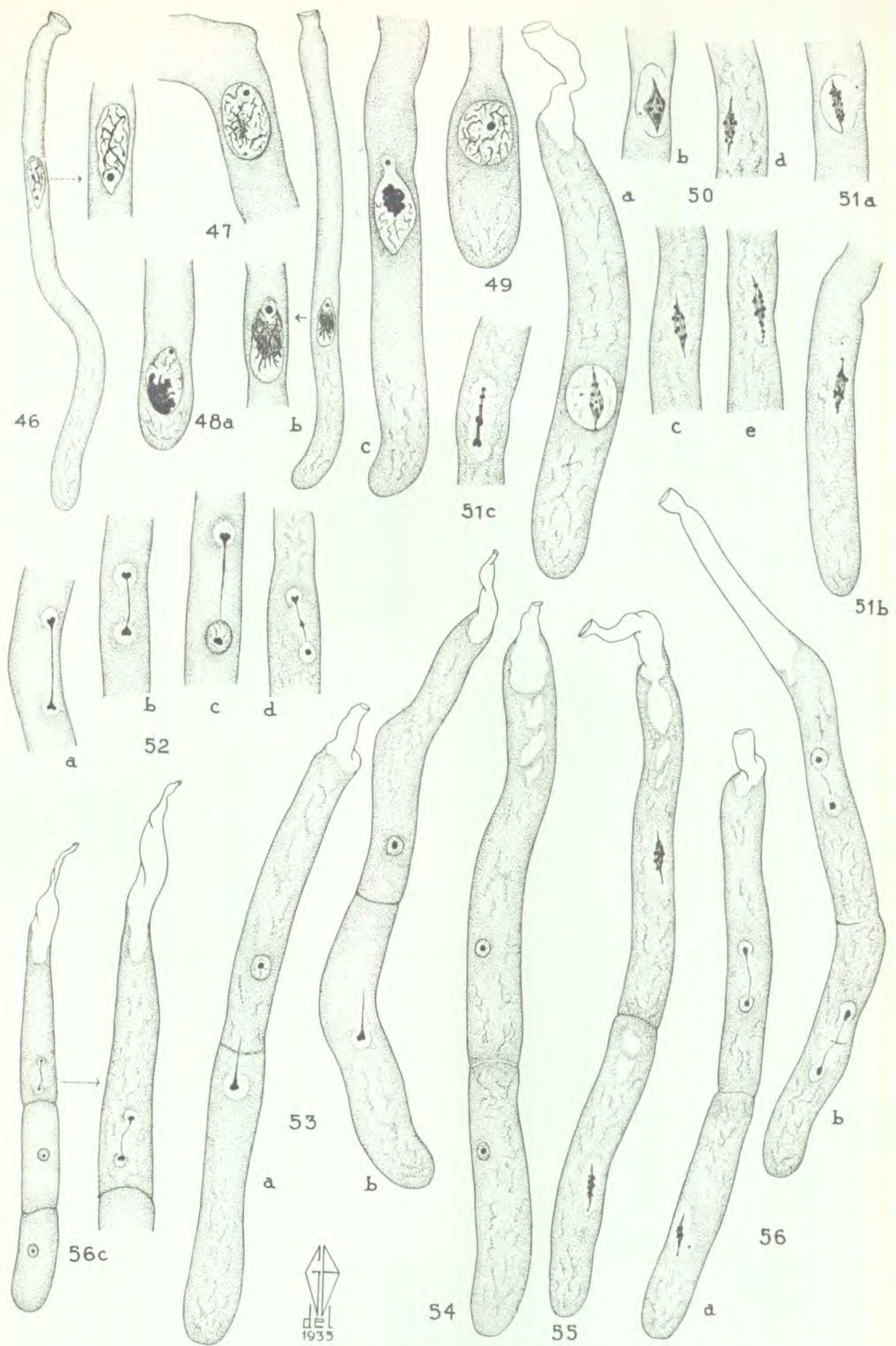
Fig. 52. Telophase. c, chromosomes massed at the poles, the two groups still connected by distinct fibers, daughter nuclei organizing; b, daughter nuclei more prominent and the fiber connections diminishing; c, lower nucleus nearly completely organized, the upper not so advanced; fibers prominent in upper region where they are still attached to the nucleus; d, darker area on connecting fibers indicative of wall formation. $\times 1865$.

Fig. 53. Two-nucleate stage. a, upper nucleus completely organized, lower nucleus still showing fiber connections; the wall is just coming in; b, wall just formed and the nuclei farther apart than in a. $\times 1865$.

Fig. 54. Two-nucleate stage. The nuclei are reorganized but the wall is not yet formed. A clearer zone shows its future position. $\times 1865$.

Fig. 55. Second meiotic division. Both spindles are in anaphase, the nuclear membranes have disappeared as well as the nucleoli. $\times 1865$.

Fig. 56. Variation in the synchronization of the second meiotic division. a, lower nucleus in anaphase, nucleolus distinct; upper nucleus in telophase. $\times 1865$; b, lower nucleus in telophase with fiber connections still visible and the wall coming in; upper nucleus nearly completely organized, the fibers still just discernible. $\times 1865$; c, daughter nuclei of lower segments completely formed with a wall between; basal nuclei still in telophase with connecting fibers between. $\times 1100$ with detail $\times 1865$.



BAKER — HELICOGLOEA

EXPLANATION OF PLATE

PLATE 11

Helicogloea Lagerheimi

Fig. 57. Four-nucleate, four-septate epibasidium, two of the walls having just been formed. $\times 1865$.

Fig. 58. a, fourth segment of epibasidium with a basal septum; b, fourth segment with protoplasmic remnants simulating a septum. $\times 1865$.

Fig. 59. Segment from an epibasidium with a nucleus showing two nucleoli. $\times 1865$.

Fig. 60. Budding sterigmata. The wall is not completely formed between the two end cells. $\times 1865$.

Fig. 61. Sterigma with spore developing on the second segment of the epibasidium. $\times 1865$.

Fig. 62. Sterigmatic formation. In segments 2 and 3 the nuclei are changing form preparatory to passing into the spores. $\times 1865$.

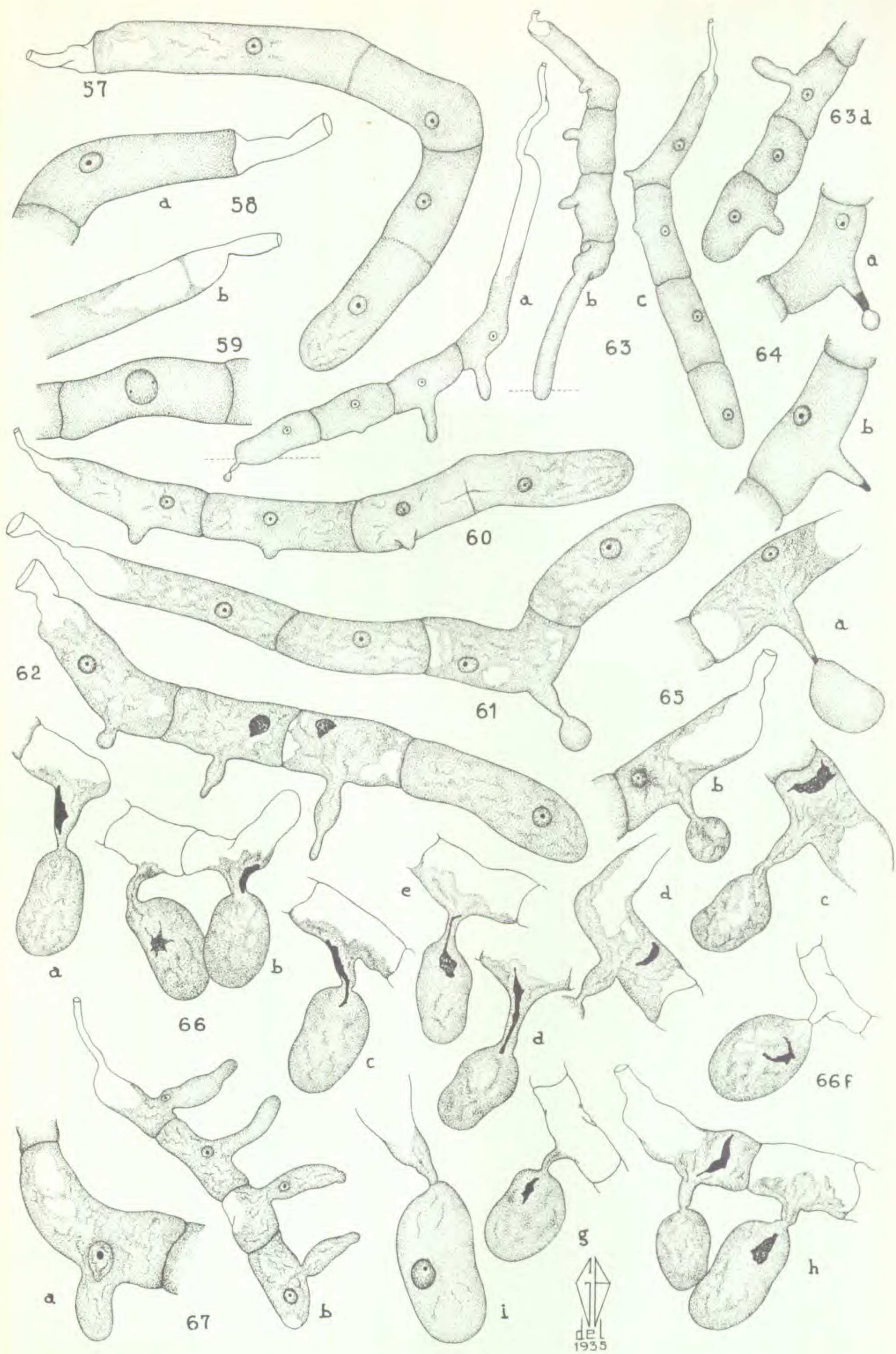
Fig. 63. Variations in sporogenous portion of the epibasidium. a, apical segment with typical sterigma; lower segments developing longer appendages; surface level marked; b, apical segment producing long appendage; surface level marked. Note the bend in the basal segment. c, sterigmatic initiation in the fourth segment; d, sterigmata forming on opposite sides. All $\times 1100$.

Fig. 64. a, b, developing sterigmata with dark staining tips. $\times 1865$.

Fig. 65. Nuclear behavior preparatory to passage into the spores. a, nucleus normal, spore about half developed. Note that the dark-staining tip is still apparent; b, nucleus becoming deeply stainable; protoplasm withdrawing into the developing spore; c, nucleus dark-staining, irregular, attenuate; d, nucleus a homogeneous dark mass. All $\times 1865$.

Fig. 66. Nuclear passage into the spore. a, nucleus in sterigma; b, nucleus of end segment, in sterigma; second segment completely drained of protoplasm and nucleus reorganizing in the spore; c, d, nuclei much drawn out in passage through the sterigmata; e, nucleus mostly within the spore; f, g, nuclei not yet reorganized in the spores; h, one nucleus reorganizing in the spore, nucleus of the basal segment ready to migrate; i, nucleus reorganized in the spore. All $\times 1865$.

Fig. 67. a, nucleus moving into a long appendage without change in form. $\times 1865$; b, sporogenous portion of an epibasidium, all segments of which have produced long appendages. $\times 1100$.



BAKER — HELICOGLOEA

EXPLANATION OF PLATE

PLATE 12

Helicogloea Lagerheimi

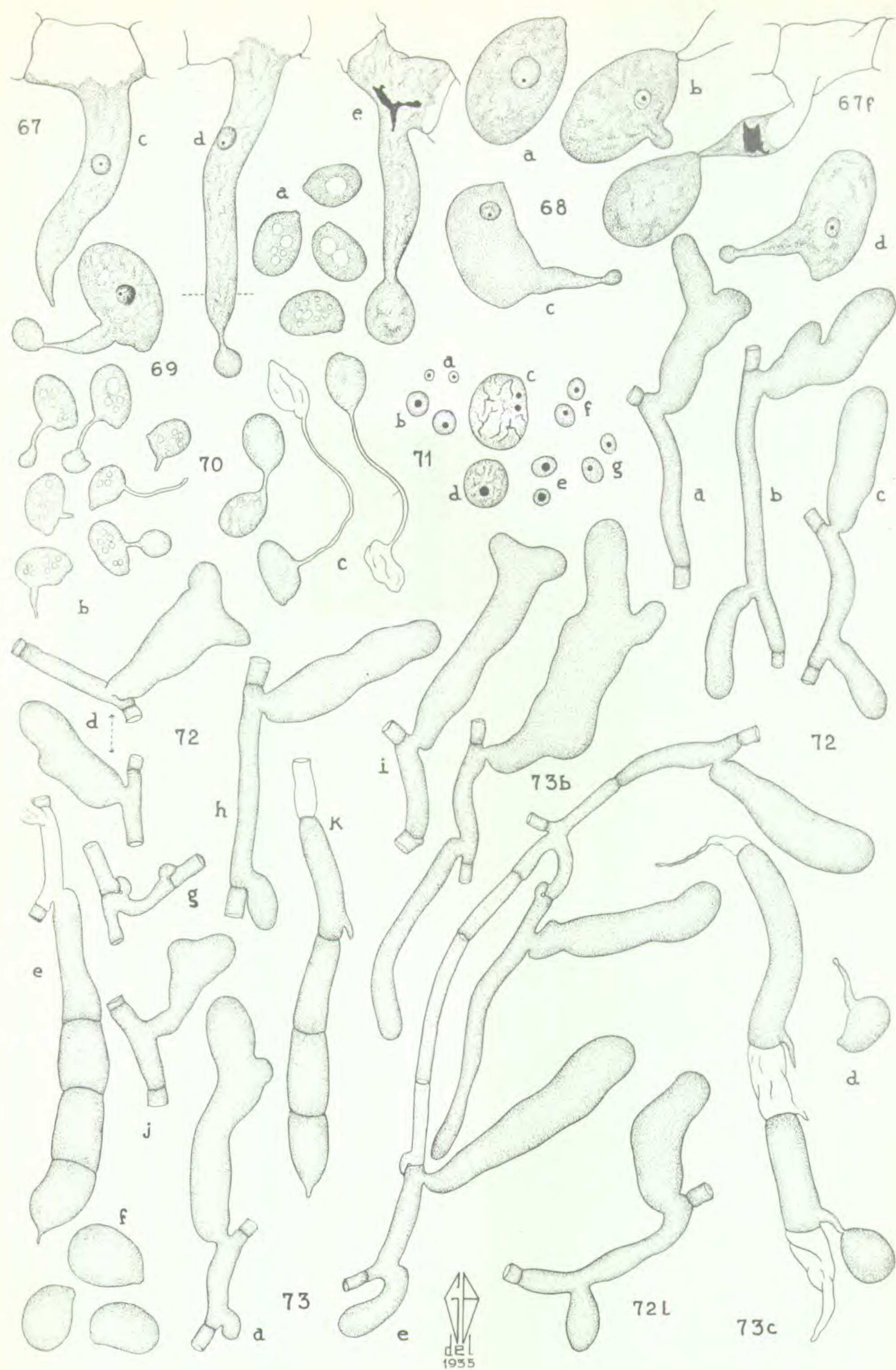
Fig. 67. c, d, formation of sterigmata and spores at the ends of long appendages. Nucleus unchanged at this stage. Surface level marked in d; e, f, nuclei prematurely changed for passage into sterigmata and spores. All $\times 1865$.

Fig. 68. a, typical spore; b, spore germinating while still attached to the sterigma; c, d, germination by repetition. $\times 1865$.

Fig. 69. Nucleus changing for passage through germ tube and sterigma into secondary spore. $\times 1865$.

Fig. 70. Germination of spores in hanging-drop cultures. a, stages prior to germ tube production, 24 hours; b, production of germ tubes and secondary spores, 24–48 hours; c, protoplasm withdrawn into secondary spores, 72 hours. All $\times 734$.

Fig. 71. Nuclei showing varying sizes through the cycle and corresponding nucleolar volumes. All from the same section and $\times 1865$. a, dikaryon from terminal hyphal cell; b, dikaryon prior to migration into hypobasidium; c, fusion nucleus in hypobasidium; d, post-fusion, nucleus contracting, nucleolar volume obviously increased; e, nuclei from migrating stages after fusion; f, nuclei from 4-celled stage of epibasidium, prior to sterigmatic formation; g, nuclei from typical spores.



BAKER — HELICOGLOEA

EXPLANATION OF PLATE

PLATE 13

Fig. 72. *Helicogloea pinicola*, No. 20124. a, forked hypobasidium; b, budding epibasidium sub-apical in position; c, budding epibasidium slightly sub-apical in position; d, typical hypobasidia; e, septate epibasidium; f, spores; g, clamp connections on the hyphae.

No. 20555. h, slightly constricted hypobasidium; i, j, forked hypobasidia; k, septate epibasidium with a fourth septum present; l, sub-apical epibasidium. All figures $\times 434$.

Fig. 73. *H. pinicola* f. *alniviridis*. a, origin of epibasidium, hypobasidium forked; b, irregular hypobasidium, typical epibasidium; c, septate epibasidium, two segments of which are already discharged; d, germinating spore; e, proliferation of basidia. All $\times 434$.

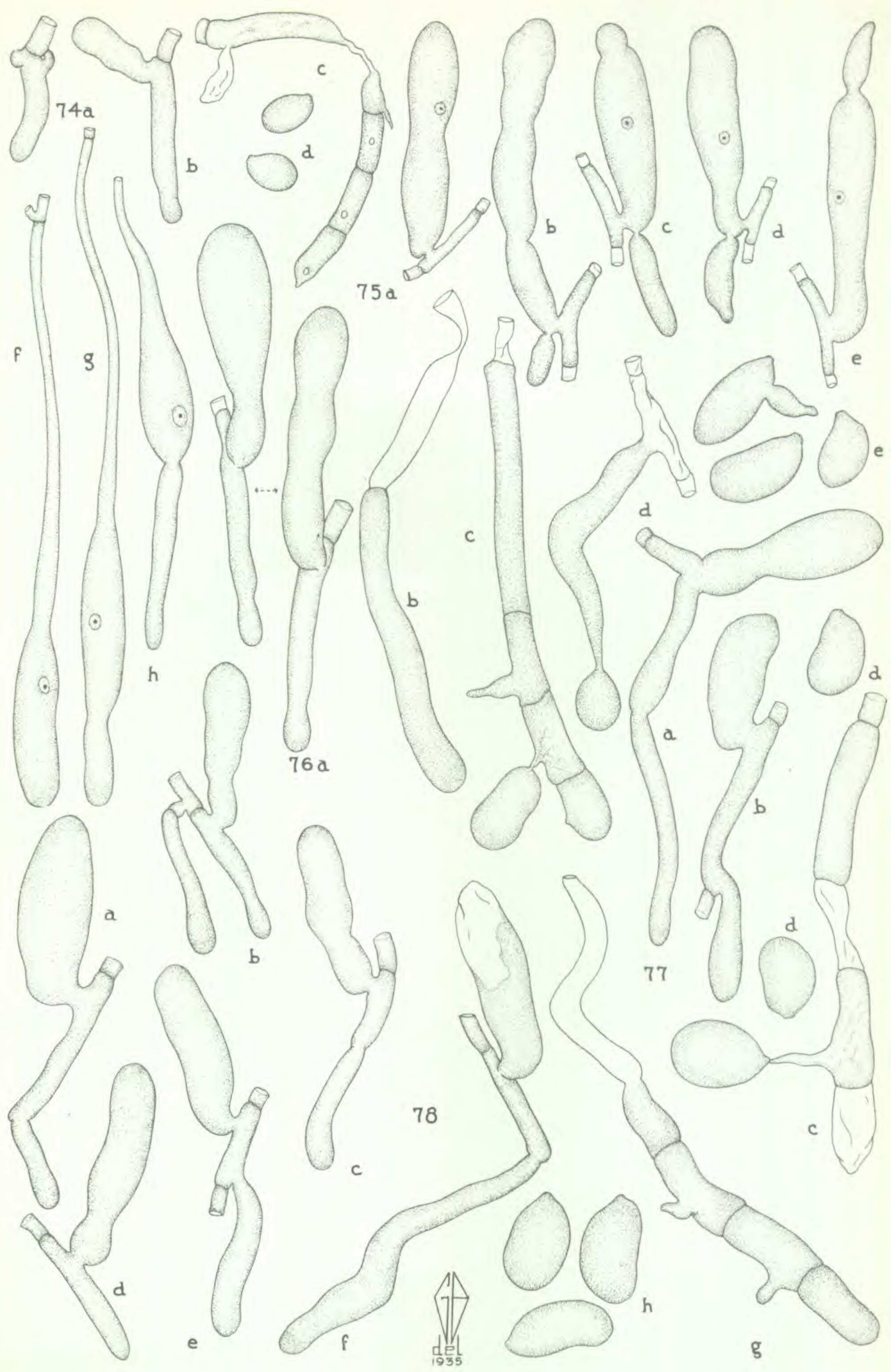
Fig. 74. *Helicogloea graminicola*. a, origin of the hypobasidium; b, mature hypobasidium; c, septate epibasidium. Note that all the protoplasm has not withdrawn from the hypobasidium. d, spores. All $\times 434$.

Fig. 75. *Helicogloea intermedia*. a, constricted hypobasidium; b, origin of the epibasidium, hypobasidium much constricted; c, basal constriction of hypobasidium; d, typical origin of epibasidium; e, proximal production of epibasidium or basal constriction; f, g, h, stages in the development of the clavate type of hypobasidium. All $\times 734$.

Fig. 76. *Helicogloea caroliniana*. a, variation in the hypobasidium; b, epibasidium; c, epibasidium with developing sterigmata and spore; d, long appendage with sterigma and spore; e, mature spores. All $\times 1100$.

Fig. 77. *Helicogloea Lagerheimi*, No. 42262, marked as var. *vulgaris*. a, constricted hypobasidium, typical epibasidium of terminal origin; b, intercalary origin of the basidium; c, septate epibasidium with four septa; two segments have already discharged their spores; d, spores. All $\times 1100$.

Fig. 78. *Helicogloea Lagerheimi*, Rick's material. a, typical hypobasidium and epibasidium; b, c, d, variously constricted hypobasidia; e, intercalary origin of basidium; f, developing sporogenous portion of epibasidium; g, epibasidium developing sterigmata; h, spores. All $\times 1100$.



BAKER — HELICOGLOEA

EXPLANATION OF PLATE

PLATE 14

Helicogloea Lagerheimi, type material

Fig. 79. a, terminal primordium and hyphae; b, slightly older primordium with origin of hypobasidium; c, hypobasidium more advanced; d, hypobasidium unusually far forward on primordium; e, large, constricted hypobasidium; f, short broad hypobasidium; g, long slender hypobasidium; h, unusually long hypobasidium. All $\times 1100$.

Fig. 80. a, epibasidium just distinguishable; b, epibasidium slightly more advanced; c, epibasidium elongating, hypobasidium emptying; d, epibasidium prior to thickening of sporogenous portion; e, sporogenous portion two-celled; f, sporogenous portion four-celled; g, sporogenous portion four-septate with sterigmata. All $\times 1100$.

Fig. 81. a, four spores; b, three germinating spores; c, one large, one small spore. All $\times 1100$.